BIOLOGICAL DIVERSIFICATION AND ITS CAUSES[1]

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ABSTRACT

Three major patterns of diversity are defined and a general hypothesis proposed to explain them. These patterns include (a) macroevolutionary diversity, encompassing temporal changes in species richness within and among clades, (b) global diversity, in which gradients of diversity among communities or biotas vary spatially and temporally, and (c) Phanerozoic diversity, which describes large-scale temporal variation in species richness within the entire biosphere. Current explanatory hypotheses for these patterns are generally formulated for systems that are assumed to be in a state of ecological equilibrium, with speciation and extinction rates being diversity-dependent. This paper describes an alternative model of diversification in which speciation and extinction rates are independent of standing diversity.

It is postulated that speciation rate is controlled primarily by large-scale changes in lithospheric (geomorphological) complexity. This hypothesis is a deductive consequence of biological data showing that allopatric speciation is the general mode of differentiation, and of geological data showing that tectonic changes within the lithosphere are responsible for the formation of geographic and ecological barriers. This hypothesis makes a number of predictions about patterns of endemism, historical biogeography, and spatial gradients of diversity, and data consistent with these predictions are presented. Other potential regulators of speciation rate (degree of morphogenetic variability within species, behavioral-ecological variability within species, intensity of sexual selection) are discussed and their potential roles in shaping diversity patterns are evaluated. Although they may occasionally be important for explaining some intracladal patterns of diversification, they are insufficient by themselves to account for spatial patterns or long-term changes of diversity within biotas.

Extinction rate is postulated to be controlled primarily by spatial and temporal changes in environmental harshness, particularly as the latter is manifested by gradients of temperature and moisture. Considerable neontological and paleontological data suggest that change in harshness is a major factor shaping temporal and spatial patterns of diversity through its effects on extinction rate. Other causal mechanisms of extinction, particularly the tectonic elimination of habitats, may be of importance for specific groups of organisms (e.g., marine shelf communities following continent–continent collisions) at specific localities and times (e.g., near a volcanic eruption) but are not likely to play as important a role as does change in harshness.

Together, the two main controls on speciation and extinction define a diversity-independent process of diversification. The biosphere can be viewed as an open thermodynamic system that can be expected to grow in complexity (including diversity) through time as a result of the inflow of matter and energy. This increase in complexity is constrained by external factors (physical changes in the biosphere or atmosphere such as ice ages) rather than by processes intrinsic to the biosphere itself (e.g., species interactions). The temporal history of the biosphere therefore has been nonequilibrial rather than equilibrial.

Clades of organisms exhibit variation in diversity through space and time, and closely related clades often are characterized by significant differences in relative diversity. Species diversity in large-scale community assemblages (biotas) varies geographically, and the relative abundances of species are apportioned nonrandomly within and among local habitats. These and other patterns of biotic diversification have been known for a long time and biologists have fervently sought their explanation. This paper addresses this question: Can a major component of the observed variance in these patterns be explained by a single causal hypothesis?

The analysis of biological diversification has recently shifted its emphasis. For many years, particularly in the 1960s, the field was dominated by the study of large-scale and local patterns of

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species diversity, particularly from an ecological point of view. Since the early 1970s, the problem of diversification has been addressed increasingly from a taxonomic viewpoint, especially by paleontologists. This change has arisen partly as a result of a reformulation of macroevolutionary analysis, from one focusing on the adaptive transformation of organismal form to an analytical assessment of changes in diversity within and among clades (Eldredge & Gould, 1972; Stanley, 1979; Eldredge & Cracraft, 1980; and many papers in *Paleobiology*). As a consequence, the literature is now dominated by the study of speciation and extinction rates using primarily fossil taxa. Significantly, while attempting to account for patterns of diversification within clades and for temporal changes in the entire biosphere, this work has often neglected the spatial analysis of diversity.

Many explanations have been proposed for patterns of diversification, yet there has been little recognition that macroevolutionary diversity and spatial diversity might constitute a single problem. Biologists realize that complex biological patterns such as those of diversity only rarely result from single causal processes. Yet, science is an endeavor that searches for generality, and thus scientific explanations, to the extent that they are in fact general, should attempt to account for as much of the variance within a dataset as possible. In so doing, patterns not explained by that hypothesis may be identified and perhaps explained by second order causal factors.

Patterns of diversification are first-order functions of speciation and extinction. A theory of biological diversification, therefore, must begin by delineating the rate-controls of speciation and extinction. This paper advances the hypothesis that spatiotemporal changes in speciation and extinction rates describe patterns of diversification both within clades and across large-scale species assemblages. In particular, diversification is postulated to be diversity-independent, with speciation rate being a function of the rate-change in lithospheric (geomorphological) complexity and extinction rate being a function of the rate-change in environmental harshness. This hypothesis makes the claim of identifying the major causal factors shaping these diversity patterns. Other factors certainly will be of importance in particular instances, and some of these will also be discussed below. Intra- and intercladal changes in species abundances and large-scale spatial gradients in diversity constitute the domain of the hypothesis, and it makes no attempt to account for local, among- or within-habitat diversity. Contemporary diversification theory is based largely on the assumption that the controls of speciation and extinction are diversity-dependent. The theoretical basis of diversity-dependent models has been evaluated elsewhere (Cracraft, in prep.) and will not be considered in detail here.

Biotic Diversification

THE PATTERNS

Patterns of diversity (species richness) can be expressed in terms of the diversifying lineages (clades) themselves, in which case these can be called macroevolutionary patterns (Eldredge & Cracraft, 1980; Cracraft, 1982a), or they can be characterized spatially as a statistical summation of all the cladal patterns present at one or more locations. These latter patterns of diversity will be termed global when the scale is large, and local (or ecological) when it is small.

Brief mention should be made of several assumptions underlying the recognition of diversity patterns (discussed in detail in Cracraft, 1981a, 1982a). In defining diversity, we seek to count all those taxonomic entities thought to be evolutionary units. Thus, concepts of species have important theoretical and empirical consequences. To the extent that prevailing species concepts vary from group to group, measures of diversity will not necessarily be comparable. Within much of vertebrate zoology (especially in ornithology and mammalogy), the biological species concept is widely applied (e.g., Mayr, 1963, 1969). That this species concept cannot be used to describe diversity accurately is not generally understood. Many differentiated, evolutionary taxonomic units, for example, can be included within a single "biological species," and this often occurs in practice (Rosen, 1978; Cracraft, 1983a). Use of the biological species concept significantly underestimates the numbers of taxa that have diversified. It is more appropriate, therefore, to adopt a species concept that is defined in terms of the evolutionary units themselves and thus accurately describes their relative abundances, both phylogenetically within clades and ecologically within and among biotas (for one such concept, see Nelson & Platnick, 1981, and Cracraft, 1983a).

Patterns of diversity can be described accurately only to the extent that highly corroborated

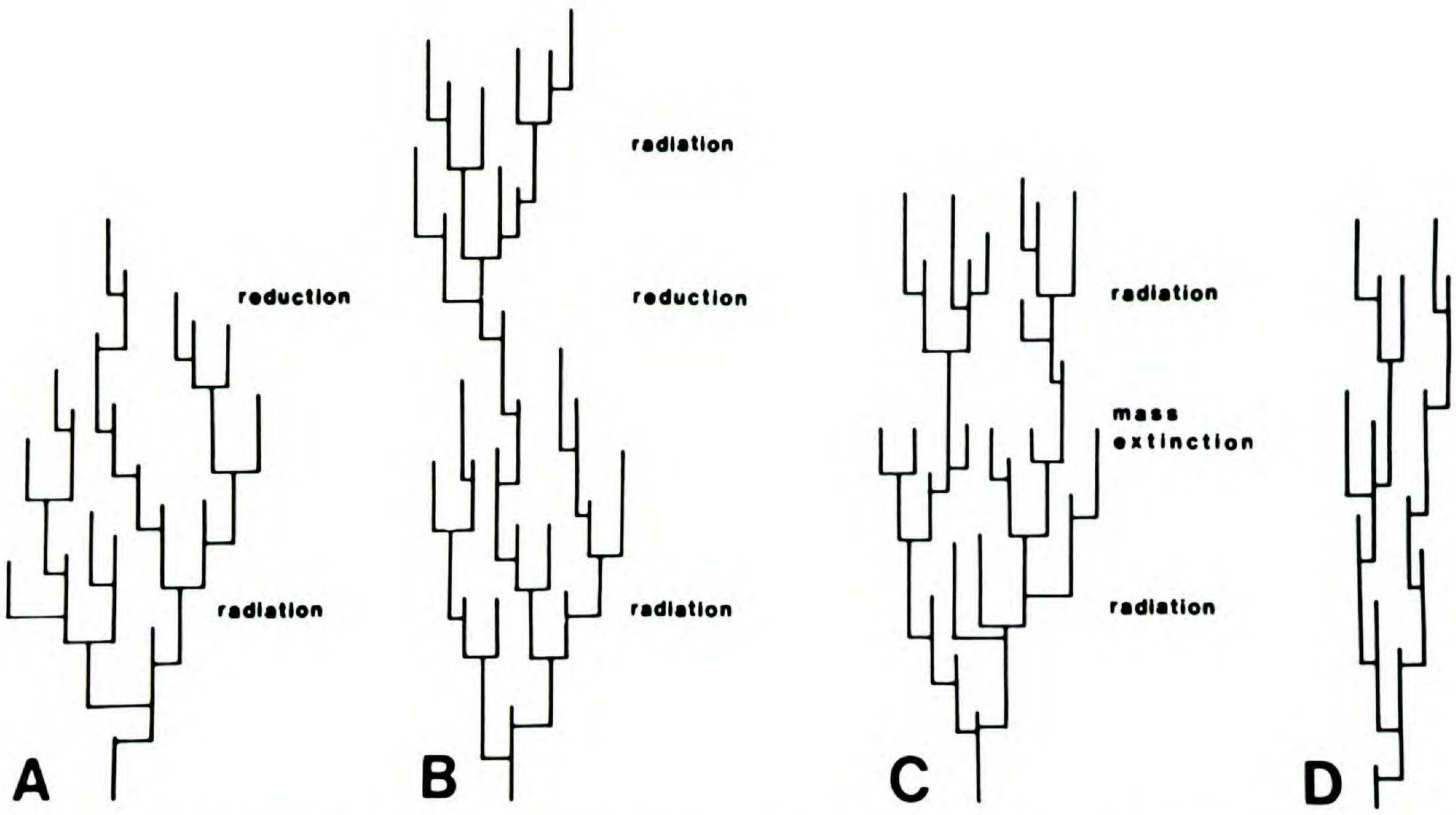

FIGURE 1. Four common patterns of diversity observed within lineages. Patterns A–C involve combinations of radiation and reduction diversity; pattern D illustrates steady-state diversity (after Cracraft, 1982a).

phylogenetic relationships are available. This is especially true with respect to macroevolutionary patterns, which are defined in terms of those relationships. Different hypotheses of relationships can change patterns of diversity significantly (Cracraft, 1981a, 1982a; Novacek & Norell, 1982). Knowledge about phylogenetic relationships may be less critical when diversity of biotas is being measured, unless that measure is being partitioned taxonomically or examined historically.

Three major kinds of diversity patterns will be addressed in this paper:

1. *Macroevolutionary diversity.* This includes patterns of species richness within and among clades. Intra-cladal patterns are expressed in terms of *radiation diversity,* in which species numbers increase with time; *reduction diversity,* in which numbers decrease with time; and *steady-state,* in which diversity is maintained relatively constant throughout time. These patterns may occur in combination within any one clade (Fig. 1).

A second macroevolutionary pattern describes sister-clades that vary greatly in relative diversity (Table 1). Because they are hypothesized to be sister-groups, the diversity of the two clades can be compared in terms of the same age of origin.

2. *Global diversity.* Large-scale gradients of species richness among communities constitute a well-known pattern, particularly as it is expressed in terms of latitude, but longitudinal gradients also exist. Many such patterns have been described in the literature (e.g., Fischer, 1960; Stehli, 1968), and some will be discussed below.

3. *Phanerozoic diversity.* Temporal variation in species richness within the biosphere has been extensively studied, particularly for marine organisms (Raup, 1972, 1976a, 1976b; Sepkoski, 1976, 1978, 1979).

EQUILIBRIUM OR NONEQUILIBRIUM?

Current models of diversification generally have borrowed their conceptual framework from population ecology. Speciation rate is analogized with birth rate, extinction rate with death rate. Then, assuming an upper limit to diversity, speciation and extinction rates are taken to be diversity-dependent, with species richness attaining an equilibrial value. The impetus for this approach, even in those studies examining patterns over vast stretches of time, appears to have been the widespread acceptance of island biogeographic theory (MacArthur & Wilson, 1963, 1967). The use of diversity-dependent, equilibrial models is pervasive, and they have been applied whether the system under discussion is diversity within the entire biosphere through the Phanerozoic (Stehli et al., 1969; Sepkoski, 1976,

TABLE 1. Some avian and mammalian sister-taxa showing significant differences in diversity probably related to tachytelic and bradytelic rates of speciation.

	Tachytelic Taxon	Bradytelic Taxon
Aves[a]	Pelecaniformes	
	other pelecaniforms (59)	Phaethontidae (3)
	Ciconiiformes	
	Ardeiidae (62)	Balaenicipitidae (1)
	Anseriformes	
	Anatidae (147)	Anhimidae (3)
	Falconiformes	
	Accipitridae + Falconidae (279)	Pandionidae (1)
	Galliformes	
	Cracidae + Phasianidae (256)	Megapodiidae (12)
	Gruiformes	
	Rallidae (142)	Heliornithidae (3)
	Columbiformes	
	Columbidae (306)	Pteroclididae (16)
	Cuculiformes	
	Cuculidae (129)	Musophagidae (18)
	Strigiformes	
	Strigidae (135)	Tytonidae (11)
	Piciformes	
	Picidae (204)	Indicatoridae (16)
	Passeriformes	
	other suboscines (1,097)	Acanthisittidae (4)
	Furnariidae (218)	Dendrocolaptidae (52)
	Laniidae (74)	Vangidae (13)
	Corvidae (106)	Grallinidae (4)
	Estrildidae (136)	Bubalornithidae (2)
	Estrildini (113)	Viduini (10)
Mammalia[b]	Chiroptera (981)	Dermoptera (2)
	Rodentia (1,728)	Lagomorpha (66)
	Rodentia + Lagomorpha (1,794)	Macroscelidea (21)

[a] For a discussion of these interrelationships see Cracraft (1981b).
[b] For a discussion of these interrelationships see Novacek (1982).

1978, 1979, 1984; Raup, 1976a, 1976b; Raup et al., 1973; Simberloff, 1974; Webb, 1976; Gould, 1976; Stanley, 1979; Valentine, 1980; Carr & Kitchell, 1980) or diversity within Recent communities (Hutchinson, 1959; MacArthur, 1965, 1972; MacArthur & Wilson, 1963, 1967; Wilson, 1969; Terborgh, 1973; Saunders & Bazin, 1975; Rosenzweig, 1975; Levinton, 1979; Fowler & MacMahon, 1982).

The use of diversity-dependent, equilibrial models has influenced our understanding of diversification in two ways:

1. *By an expectation of pattern.* Observations are theory-laden and our expectation of patterns in nature is dependent on the predictions of our theoretical worldview. By building an equilibrial viewpoint into diversification models, however, expected and observed patterns are more likely than not to confirm (and conform to) that viewpoint. Thus, many paleontologists have interpreted the Phanerozoic diversity curve to be equilibrial (e.g., Sepkoski, 1978, 1979; see Discussion), with mass extinctions perturbing diversity away from the equilibrium, but only for relatively short periods of time. Likewise, the expectation of pattern is also prevalent when diversity-dependent models are applied to patterns of species diversity at the local level. Some of these latter observational expectations include: saturation of habitats, competitively structured community assemblages, predominance of density-dependent mortality, and the presence of limiting similarities among co-existing species, to name only a few (see Wiens, 1984, for further examples and discussion).

Perhaps the major expectation (or assumption) of diversity-dependent models is that there is an upper limit to diversity (MacArthur, 1969; Margalef, 1972; Van Valen, 1976; Levinton, 1979). The upper-limit hypothesis has its strongest rationale within current ecological theory when attempts are made to explain within-habitat diversity, but it also has been extrapolated to the biosphere as a whole. I will return to this hypothesis in the Discussion.

2. *By an expectation of process.* Underlying assumptions also carry with them explicit expectations about the causal structure of nature. As noted, acceptance of an equilibrial worldview has resulted in the widespread use of diversity-dependent models of speciation and extinction rate-control. Metaphorically speaking, the biosphere is viewed as a large *Tribolium* population bottle, in which space and resources are assumed to be limited; then, using the same logistic growth equations of population biology, paleontologists have extended the analogy to expect a decrease in speciation rate and rise in extinction rate with increasing diversity (MacArthur, 1969; Valentine, 1973; Rosenzweig, 1975; Sepkoski, 1978; Carr & Kitchell, 1980). Diversity-dependent "control" of these rates is postulated to result directly from intensified ecological interactions as diversity increases, in particular increased competition and species packing, along with reduced dispersal ability (see above cited authors for a more detailed explanation and Cracraft, in prep. for a critical evaluation of this model).

The hypothesis presented here states that the patterns and processes of biological diversification are more properly characterized within a diversity-independent, nonequilibrial framework. There are several reasons for applying this conceptual approach to questions within evolutionary biology. One is that historical systems, whether physical or biological, behave as if they are nonequilibrial rather than equilibrial, and therefore it seems appropriate that their description be cast in nonequilibrial terms (Mercer, 1981; Peacocke, 1983). Biological systems, including individual organisms, species, communities, and the biosphere, appear to exhibit a transformational history of increasingly more organized steady-states; with rare exceptions, they increase in complexity through time. Thus, an increasing number of biologists have applied nonequilibrial ideas to questions about the origin of macromolecular complexity (Prigogine et al., 1972; Saunders & Ho, 1976, 1981; Wicken, 1978, 1979, 1980; Eigen, 1971; Eigen & Schuster, 1977, 1978a, 1978b), general evolutionary theory (Wiley & Brooks, 1982; Brooks & Wiley, 1984), developmental biology (Zotin, 1972; Lurie & Wagensberg, 1979), and community structure and evolution (Gallaucci, 1973; Ulanowicz, 1980; Phipps, 1981; Johnson, 1981).

A second reason for considering a nonequilibrial approach is that it creates an alternative way of conceptualizing or modeling evolution. Nonequilibrial systems are inherently transformational and nongradualistic when seen macroscopically (Mercer, 1981; Wiley & Brooks, 1982). In contrast, equilibrial systems, by their nature, are not persistently transformational, and within this conceptual framework biologists frequently have constructed elaborate hypotheses to explain the "forces" maintaining the system at or near equilibrium, or returning that system to equilibrium following a perturbation by some outside "force." A nonequilibrial viewpoint places the description of biological systems behavior in a new light.

THE DIVERSITY-INDEPENDENT RATE-CONTROL OF SPECIATION

The primary aim of this section is to describe a hypothesis of speciation rate-control that is diversity-independent. Other factors have also been hypothesized to modulate the rate of speciation, and these will be discussed separately.

THE HYPOTHESIS OF LITHOSPHERIC COMPLEXITY

That speciation rate is controlled primarily by nonequilibrial changes in large-scale lithospheric (geomorphological) complexity can be deduced from biological and geological premises. The hypothesis itself can then be used to generate testable predictions about patterns of biological diversification. Consider two biological and two geological premises:

Premise 1. Speciation is a geographical phenomenon and is allopatric in most groups of organisms (Mayr, 1963; Grant, 1971; Bush, 1975; White, 1978).

Speciation via genetic alterations such as polyploidy is frequent in some groups, particularly angiosperms (Grant, 1971; White, 1978), but there is little evidence to suggest that allopatric differentiation is also not prevalent in these taxa. In both plants and animals, sister-species are usually observed to be allopatric. For example, within tephritid flies of the genus *Rhagoletis,*

which has been studied extensively because it is said to provide a possible example of sympatric speciation, most of the species are allopatric and almost certainly exhibited geographic disjunction during their diversification [Bush (1966); see also the arguments of Futuyma & Mayer (1980) against the commonness of non-allopatric differentiation].

Premise 2. Allopatric speciation is dependent upon the origin and maintenance of geographic or ecological barriers.

This assumption is straight-forward and empirically well-corroborated (Mayr, 1963; Bush, 1975; White, 1978). Geographic barriers are important in two ways, by promoting vicariance and isolation of widespread populations and by providing the possibility of isolation given long-distance dispersal across those barriers. Although not dependent upon an assumption about the relative frequencies of vicariance and long-distance dispersal, the hypothesis can be used to predict spatial characteristics of differentiation (see below).

Premise 3. The lithosphere is an irreversible thermodynamic system exhibiting a nonequilibrial increase in complexity.

Decay of radioactive isotopes of uranium, thorium, and potassium produces heat that ultimately drives mantle convection currents and lithospheric plate motion (Davies & Runcorn, 1980; Bott, 1982). Being a historical system, the lithosphere is irreversibly transformational. Geological degradation of complexity may occur locally (for example, from erosional processes), but the overall historical trend has been for complexity to increase globally, as evidenced by our ability to reconstruct past lithospheric (geomorphological) configurations.

Premise 4. The rate of formation of geographic and climatic barriers is a function of rate-changes in lithospheric (geomorphological) evolution.

Relative plate motions create large-scale geomorphological complexity in some areas and contribute to processes of geological degradation in others. Regions of high complexity (e.g., areas of high relief) are generally associated with highly active, converging plate margins or with active deformation within plates. Changes in the lithosphere also have first-order effects on climatic change (Hamilton, 1968; Cox, 1968; Crowell & Frakes, 1970; Frakes & Kemp, 1972, 1973) and thus on the rate of climatic barrier formation.

These premises lead to the hypothesis that *the rate of speciation is a first-order function of lithospheric (geomorphological) complexity.* A causal connection between speciation and large-scale plate motions has been suggested before (see especially Valentine & Moores, 1970, 1972; Valentine, 1971, 1973; Bakker, 1977). Simpson (1964) and Nel (1975) also noted a correlation between geologic (topographic) complexity and diversity, thereby inferring a relationship to speciation. Bakker (1977) postulated cycles of orogeny and marine transgressions producing cycles of speciation in the highlands of continents, with subsequent immigration (dispersal) of species into lowland habitats. Ross (1972), in a highly stimulating and underappreciated paper, viewed diversification as a rate-function of geographic disjunction within a nonequilibrium biosphere; his short contribution is one of the more explicit statements to date regarding the rate-control of speciation by earth history.

The hypothesis of lithospheric complexity described here differs significantly from this previous work. It states explicitly that the rate-change of geological complexity is the primary control of speciation rate. The hypothesis also makes a larger claim: because the lithosphere exhibits a nonequilibrial increase in complexity through time, Phanerozoic patterns of diversification should also be nonequilibrial. Furthermore, the hypothesis is more general: although it acknowledges the correlation between high topographic relief and high diversity, it posits a causal relationship between lithospheric complexity and speciation rate across both terrestrial and marine environments. Thus, topographic relief per se is not the central causal agent of speciation control; rather, it is the rate-change in geomorphological complexity that is causally related to the rate at which barriers arise and taxa therefore speciate. Areas of high relief may be geologically stable and produce few species, whereas areas of lower relief may be tectonically active and produce species at a higher rate.

We now turn to some predictions and implications of the hypothesis of lithospheric complexity and examine observational data relevant to them. Critical problems exist with any attempt to decipher the causal mechanics of diversification. If we are examining the expected influence of a particular causal hypothesis (as with lithospheric complexity, for example), not only are there the confounding contributions of other factors controlling the rate of speciation, but also

the concomitant effects of extinction. Except under very special circumstances, we cannot expect to measure speciation rates directly and accurately. Consequently, diversity patterns themselves constitute the data with which we must test alternative causal processes. However, diversity patterns are the end result of the spatiotemporal history of all the separate causes of speciation *and* extinction. Therefore, predictions derived from any one hypothesis of speciation or extinction rate-control must of necessity be proposed within the context of *ceteris paribus*. This requirement naturally raises the specter of ad hoc escapes from potentially conflicting observational data: if the data do not fit the hypothesis being tested, are we to claim that the hypothesis itself is not rejected because deviations from expectation can be ascribed to other causal factors? This onerous problem can rarely be avoided when many causal factors are involved; one can only attempt to discuss its ramifications as openly as possible (e.g., see Hillborn & Stearns, 1982). This situation does *not* mean that causal hypotheses about speciation and extinction rate-controls are untestable; as long as the relative influence of other potential causal factors can be minimized, then the importance of a specific causal mechanism can be investigated.

A series of predictions can be derived from the hypothesis that geomorphological change controls the rate of speciation, including:

Prediction 1. Species will be distributed nonrandomly and will be clustered in areas of endemism.

If geomorphological change mediates the spatial pattern and tempo of speciation, then geologically induced barriers (physiographic or ecological-climatic) will partition biotas through time, and thus produce common areas of endemism. This is a strong prediction, but the expected patterns can be obscured (1) by population dispersion in which case species ranges will exhibit varying degrees of congruence, or (2) by long-distance dispersal across barriers. If taxonomic differentiation took place *only* by long-distance dispersal and not by the vicariance of species that were already widespread, then the frequency of well-defined areas of endemism would be low. Long-distance dispersal is a stochastic property of individuals, and thus major centers of endemism are not likely to arise by this process. In summary, if areas of endemism did not exist, or were very uncommon, then the hypothesis of lithospheric complexity would not be corroborated.

Observational data strongly support this prediction. It has been known for several centuries that organisms are nonrandomly distributed and cluster in areas of endemism. The literature pertaining to areas of endemism (also termed "areas of provinciality," or "centers of dispersal") is vast. For example, well-marked areas of endemism are apparent in the avifaunas of Australia (Keast, 1961); Africa (Hall & Moreau, 1970; Snow, 1978), and South America (Muller, 1973; Haffer, 1978; Cracraft, 1985). Likewise, Gentry (1982a) and Prance (1982a, 1982b) have presented data documenting the existence of areas of endemism within the South American flora. Many more examples could be cited.

Prediction 2. Species will exhibit congruent patterns of historical biogeography.

There is no stronger test of the hypothesis of lithospheric complexity than the relative frequency of congruent biogeographic histories of clades whose species are endemic in the same areas (Rosen, 1978, 1979; Platnick & Nelson, 1978; Nelson & Platnick, 1981; Cracraft, 1982b, 1983b). The vicariance of biotas is the only known mechanism producing congruent histories involving three or more areas of endemism; the other mechanism producing allopatric disjunction, long-distance dispersal, can yield two-area congruence (as from a mainland to an island), but invoking it to explain patterns involving three or more areas necessitates accepting countless ad hoc assumptions about dispersal, the relative timing of differentiation, and extinction (see above citations).

Thus, the degree to which phylogenetic relationships of species confirm the existence of congruent biogeographic patterns is a direct estimate of the rate-control of speciation by geologic (including climatic) fragmentation. Unfortunately, the field of vicariance biogeography is still in its infancy, and few studies bearing on this prediction have been completed. Nevertheless, several investigations corroborate the hypothesis in that they have discovered congruent patterns. Rosen (1978, 1979) documents an example using Central American freshwater fishes; Cracraft (1982b, 1983a, 1983b) does likewise for some Australian birds; Wiley and Mayden (1985) also present strong evidence that vicariance was extremely important in the diversification of the eastern North American fish fauna. Finally, the Amazonian forest avifauna also presents examples of

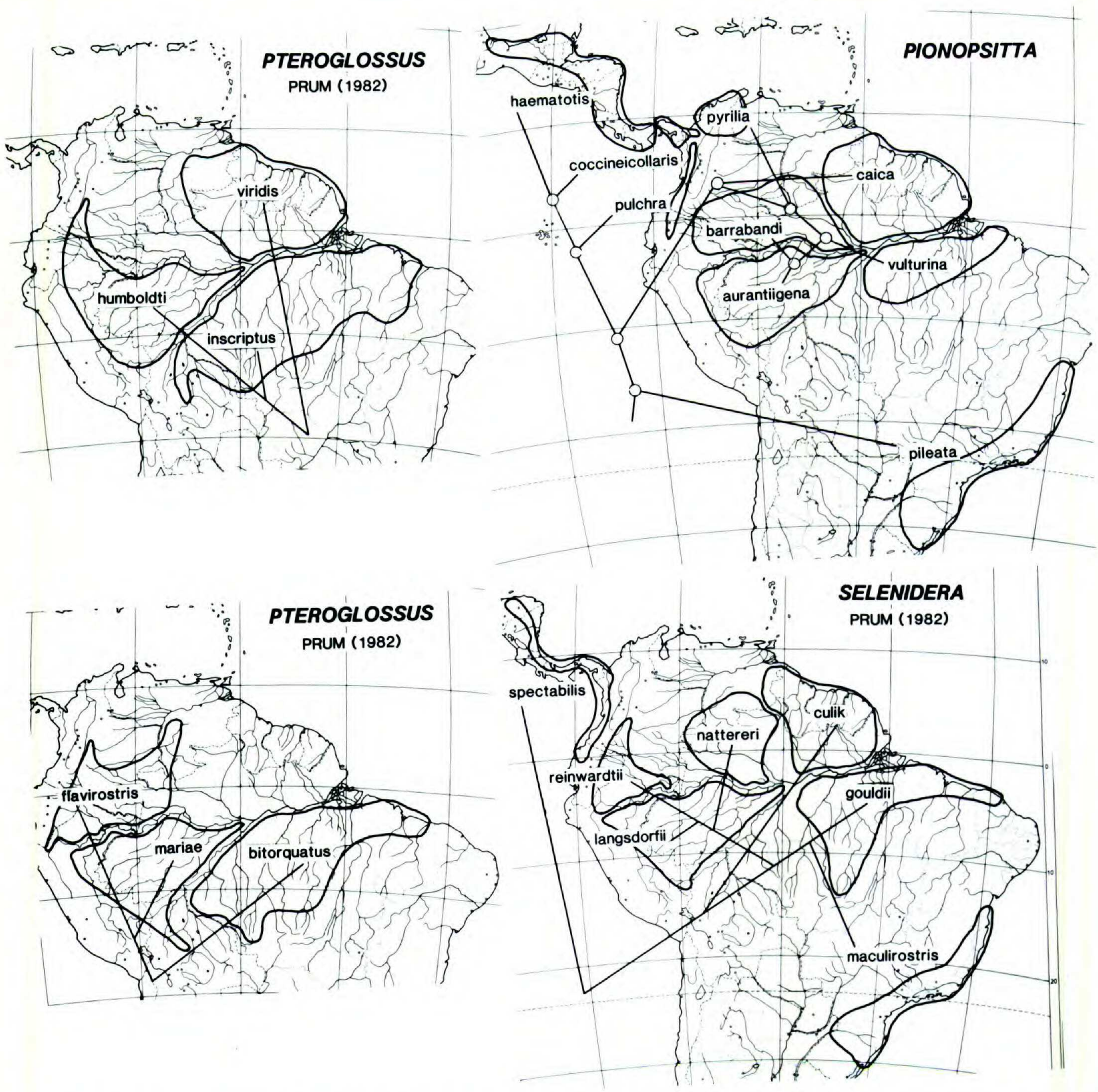

FIGURE 2. Four lineages of tropical South American birds exhibiting congruence for four areas of endemism in Amazonia. The phylogenetic patterns within these clades indicate the following pattern of historical biogeography: northeast Amazonia + [southeast Amazonia + (northwest Amazonia + southwest Amazonia)]. This congruence implies that the biota within this area was segregated via geological or ecological vicariance events (see text). Other taxa in Central America, northwest South America, and southeast Brazil represent unique components in these comparisons. Data after Prum (1982) and Cracraft (unpubl. observ.).

taxa whose biogeographic patterns are congruent with one another (Prum, 1982; Cracraft, unpubl. observ.; see Fig. 2).

Congruent biogeographic histories such as these are compelling support for the hypothesis of lithospheric complexity. That congruence implies that the biotas themselves have been fragmented by common geographic barriers, and if so, we can predict that other taxa endemic in these same areas eventually will be shown to have histories congruent with those already studied. If geological change has not set the tempo of diversification, or has played only a minor role, then biogeographic congruence should be rare or nonexistent.

Prediction 3. Geographic gradients in species diversity will parallel gradients in lithospheric complexity.

All things being equal, species diversity should be higher in regions of higher complexity. But things are rarely, if ever, equal. Regions of lower complexity might have higher diversity if extinction has been significant in those regions of higher complexity. Thus, in attempting to ex-

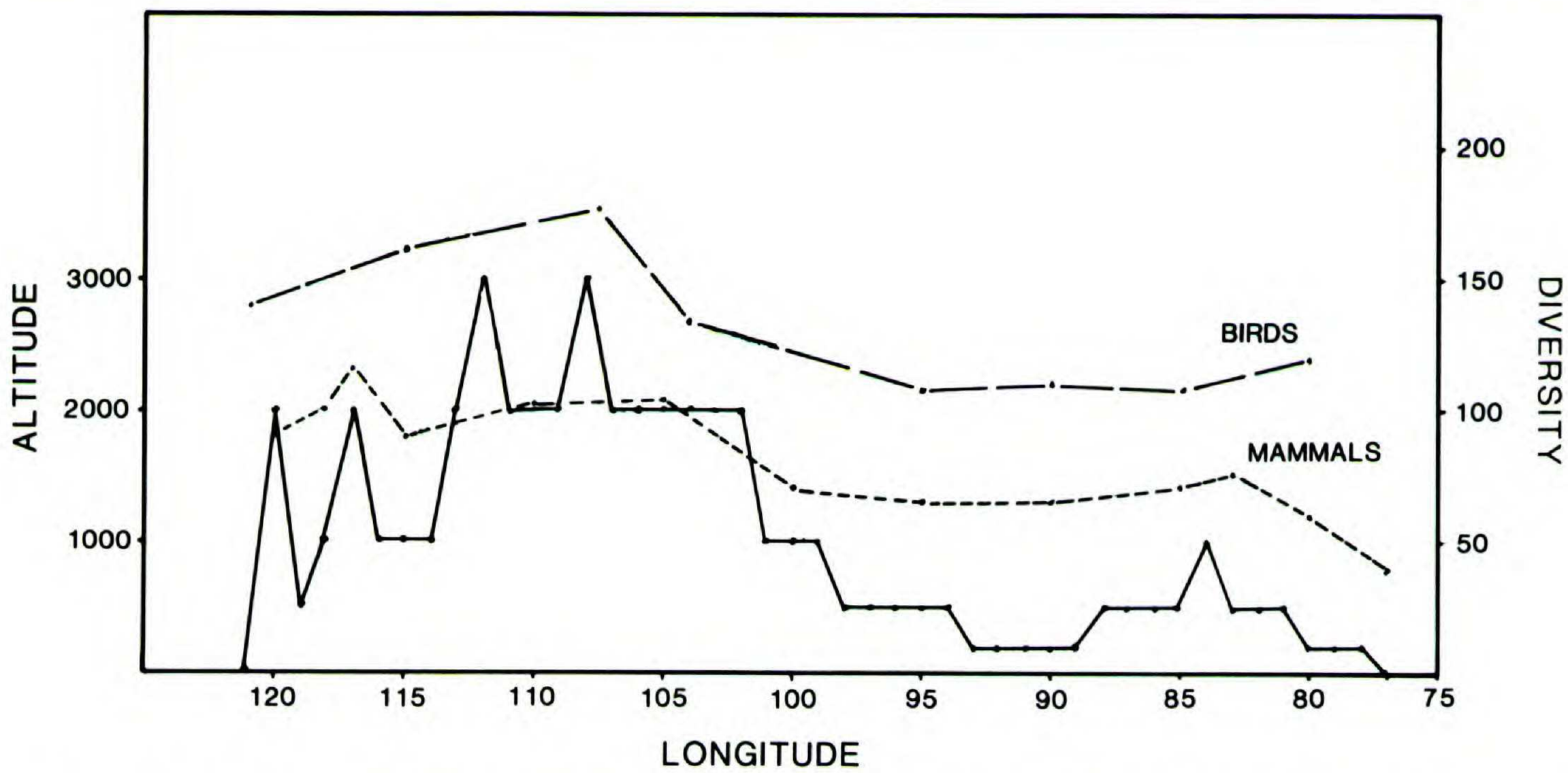

FIGURE 3. A longitudinal transect across the southern United States at 35°N latitude showing the relationship between topographic (geomorphological) complexity and species diversity gradients of birds and mammals (data from MacArthur, 1969; Simpson, 1964). Diversity in both groups rises in those areas having the greatest topographic complexity (see text).

amine this prediction, it is important to minimize the potential effects of variation in extinction along the geographic transect being investigated. As will be discussed below, this is probably one of the reasons why latitudinal transects of diversity do not show close correlation with complexity. Longitudinal transects, on the other hand, can be chosen so as to reveal the relationship between diversity and complexity while at the same time minimizing the influence of extinction in obscuring that pattern.

Consider first data from a continental setting. Figure 3 shows a longitudinal transect across the southern United States at 35°N. In this figure, relative topographic relief is taken to be an approximation of lithospheric (geomorphological) complexity. Data on species richness for mammals (Simpson, 1964; Wilson, 1974) and land birds (MacArthur, 1969; see also Cook, 1969) are also displayed. The gradient in diversity of both birds and mammals parallels the gradient in topographic complexity, as predicted by the hypothesis. [Simpson (1964: 70) noted as a "speculative possibility" the idea that high topographic relief might have promoted more speciation in the West (see also Cook, 1969).]

Comparable data for similarly chosen gradients are rare indeed, in part because the taxa being analyzed must not be sensitive to any marked change in environmental harshness along the gradient. Thus, it is not surprising that amphibians exhibit a strong westward decrease in diversity along the same transect (Kiester, 1971), and the major change in diversity corresponds to a steep decline in moisture availability in the central United States. Reptiles also exhibit a westward decrease in diversity (Kiester, 1971) but the gradient is, not unexpectedly, much less steep than that for amphibians: reptiles are, in general, less affected by arid conditions than are amphibians but are more susceptible to increases in harshness (as determined by temperature) than are birds or mammals.

The South American vertebrate fauna offers considerable potential for evaluating this prediction, but distributional data are lacking or rudimentary for most taxa. Available information, however, seems to support the third prediction. Diversity of amphibians (Lynch, 1979), reptiles (Dixon, 1979), and birds (Slud, 1976; Donahue et al., in prep.; Terborgh et al., 1984) is highest along the lower slopes of the Andes and the immediately adjacent lowlands as compared to the lowlands of the Amazonian basin itself. Moreover, as expected, diversity decreases with increasing altitude and a rise in the harshness of montane environments.

Species diversity patterns of plants, to the extent that they have been resolved, parallel the data for vertebrates. Based on current knowledge, and on projections of the numbers of species estimated yet to be discovered and described,

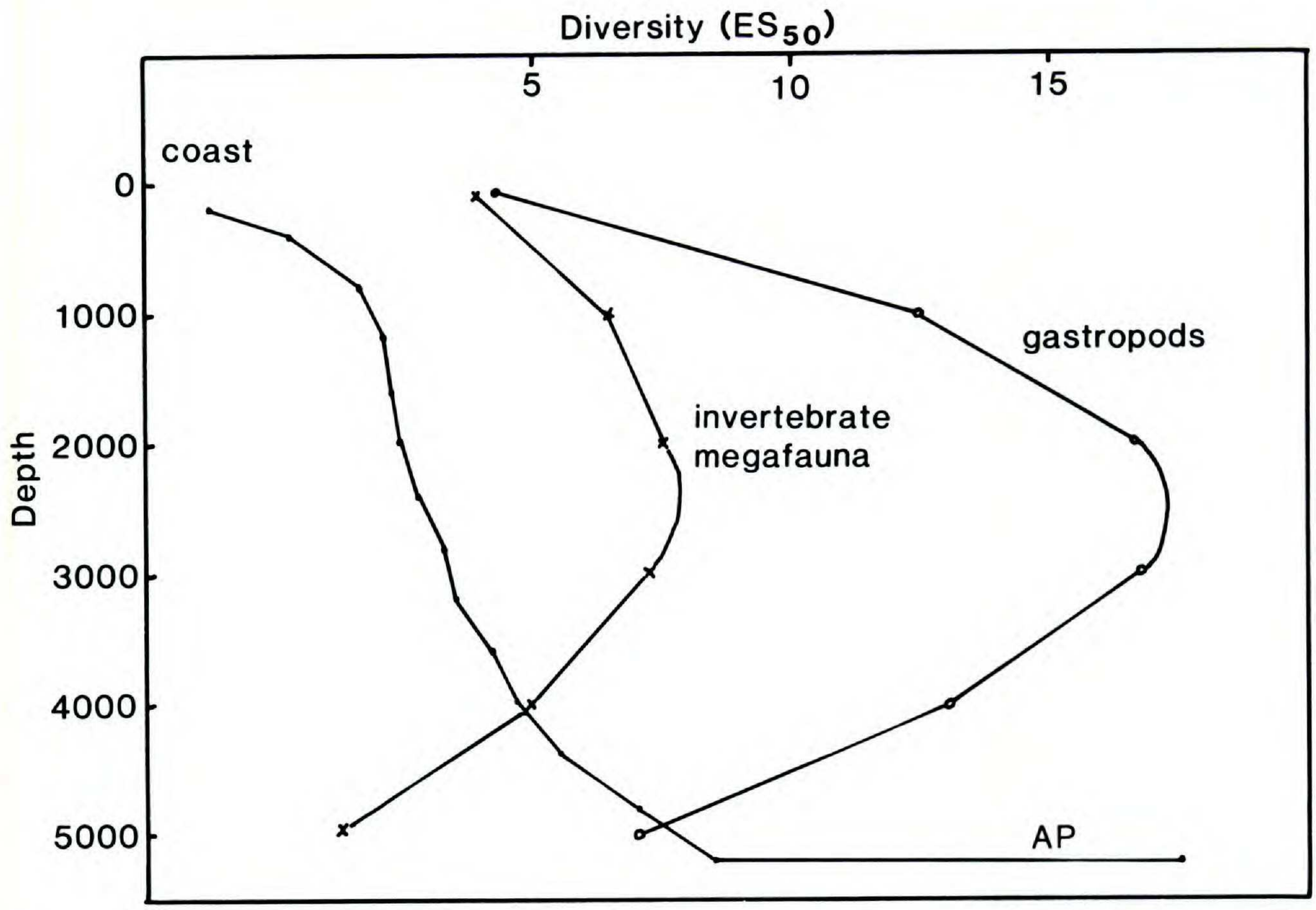

FIGURE 4. A topographic profile of the continental margin in the western Atlantic (at 35°N latitude) plotted with the expected diversity of representative invertebrate groups at the given depths (data from Rex, 1981a). The shape of the two species diversity curves is exemplary of that found in other benthic marine invertebrates. Vertical exaggeration about ×130.

plant diversity appears to be highest along the lower, tropical and subtropical slopes of the Andes when compared to the Amazonian basin (Gentry, 1982b, 1982c; pers. comm.). This must remain a tentative conclusion, of course, but the large number of species with very restricted ranges within the Andes is enormous and even many small mountain valleys harbor large numbers of narrowly endemic species.

Geographic transects of continental species diversity that are appropriate for testing this prediction are scarce and potentially susceptible to influences other than that of lithospheric complexity. Alternative ways of examining the influence of complexity on diversity will be pursued in subsequent predictions.

A further evaluation of the third prediction can be made using data from the marine realm. In this case, longitudinal transects probably exhibit less geographic variation in harshness and thus presumably show fewer effects of extinction than do transects across continents. Three patterns of diversity/complexity are relevant for the third prediction.

a. *North Atlantic diversity gradients.* From the coast, species diversity of benthic invertebrates increases on the continental slope and rise but decreases again as abyssal depths are approached (Hessler & Sanders, 1967; Sanders, 1968; Rex, 1981a). Indeed, diversity is highest for virtually all groups at depths of 2,000–3,500 meters (Rex, 1981a). Much attention has been paid to the causes of high diversity in the deep-sea (see Discussion), but one explanation has not been seriously considered, namely, increased lithospheric complexity.

The slope and upper rise represent the region where continental and oceanic crustal regimes meet. Relative to shelfs, rises, and the abyssal plain, continental slopes are more highly complex geomorphologically, with many deep submarine canyons and gullies generally traversing their flanks (e.g., Uchupi, 1968). The relationship between the continental margin profile of the North American Atlantic coast and two representative diversity profiles for marine invertebrates is pictured in Figure 4. In this figure, the profile itself does not adequately convey the complexity of the slope and upper rise sufficiently because the scale is too small.

It can be hypothesized, therefore, that increased diversity with increasing depth is related

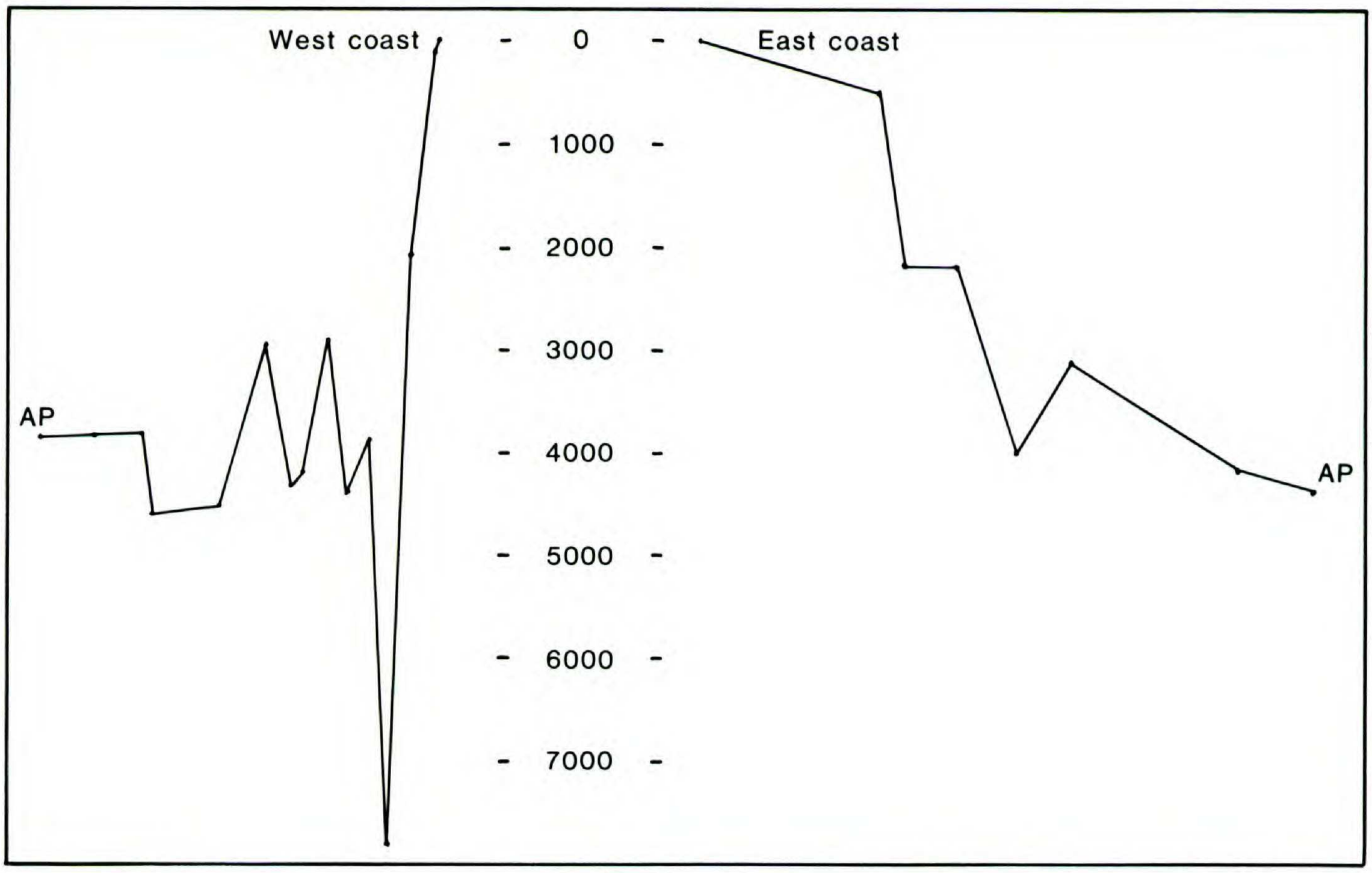

FIGURE 5. Topographic profiles of the Pacific and Atlantic continental margins of South America at 25°S latitude. The profiles begin at the coast and end at the abyssal plain (AP). The Pacific margin is tectonically active and much more complex geomorphologically than the passive margin of the Atlantic. Higher species diversity along the Pacific coast is postulated to result from increased rates of isolation in that spatially more complex region (see text). Vertical exaggeration about ×70.

to gradients in geomorphological complexity and to the opportunities that complexity creates for geographic isolation and differentiation. This hypothesis differs markedly from the prevailing ecological explanations for these diversity patterns such as the time-stability hypothesis, which will be reviewed and analyzed in the Discussion.

b. *Active versus passive plate margins.* Active plate margins such as the western coast of South America are much more complex geologically than passive margins as exemplified by the Atlantic (Fig. 5). Active margins gain their complexity from the extreme structural relief resulting from plate–plate interactions; passive continental margins, in contrast, may even degrade in complexity through time due to the deposition of continental sediments. Consequently, we would predict that active margins, which are continually changing their configuration, should promote higher diversity.

The available data seem to support the prediction. Thus, species diversity of bivalve molluscs is nearly twice as high along the western coast of South America than along the eastern coast (Stehli et al., 1967; Valentine, 1971). This pattern of diversity extends northward to North America but there the pattern is confounded by a Late Cenozoic extinction event in the western Atlantic (Stanley & Campbell, 1981).

c. *Large-scale diversity patterns of the Pacific.* The Pacific basin shows considerable variation in geomorphological complexity, from being the least complex on the abyssal plain of the central Pacific, to very highly complex in the Indo-Australian region where microplates, island arcs, and areas of subduction abound. Using this gradient in complexity as a predictor of diversity, greater diversity would be expected along the western margin of the Pacific. This is precisely what is seen.

The highest diversity of bivalve molluscs, for example, is found in Australasian waters (Stehli et al., 1967), with over 1,000 species as compared to the 150–250 species found in the central and eastern Pacific. Zooxanthellate (Rosen, 1981) and hermatypic corals (Stehli & Wells, 1971) also show greatest diversity in the western Pacific. Stehli (1968) presented data for other groups (e.g., gastropods) having a similar pattern of diversity.

Prediction 4. Large clades, widely distribut-

TABLE 2. Patterns of diversity in neotropical flycatchers (Tyrannidae) and tanagers (Thraupidae).

	Andean Region	Central American Region	Amazonian Region
Relative area	0.27	0.30	1.0
Rank order in geomorphological complexity	1	2	3
Tyrannidae[a]			
Differentiated taxa	310	177	184
Rank order	1	3	2
Differentiated taxa/genus	6.89	4.12	3.76
Thraupidae[b]			
Differentiated taxa	297	123	105
Rank order	1	2	3
Differentiated taxa/genus	9.00	6.15	5.53

[a] Data for the tyrannids from Traylor (1979).
[b] Data for the thraupids from Paynter and Storer (1970).

ed over the same areas, will exhibit covarying gradients in diversity that parallel the gradient in lithospheric complexity.

The third prediction was primarily a statement about gradients of diversity averaged over many clades, that is, a statement about biotic patterns. The fourth prediction partitions that biotic pattern and makes a statement about the causes of diversity within and among the clades themselves.

If a clade is distributed widely over an area that has significant variation in geomorphological complexity, the hypothesis of lithospheric complexity predicts diversity will be higher in regions of higher complexity. But again other causal factors must be held constant, thus we assume that taxa within the clade have been distributed in the different areas for about the same amount of time, and that extinction rates have been roughly equivalent across the entire distribution. If these assumptions are satisfied, then complexity should emerge as the primary predictor of diversity patterns.

In order to examine this prediction, two highly diverse and widespread avian families of tropical America were examined, the tanagers (Thraupidae) and the flycatchers (Tyrannidae). Three biogeographic regions, the Andes (upper part of tropical zone and above), Central America, and tropical lowland Amazonia, were chosen for comparison, with each representing an area of very high, intermediate, and low geomorphological complexity, respectively. Diversity was calculated by tabulating the numbers of endemic subspecies (in the case of polytypic species) or monotypic species in each region, following the recent systematic treatments of the Peters' "Check-list of Birds of the World" (Paynter & Storer, 1970; Traylor, 1979); subspecific, rather than species-level, taxa were ennumerated in order to estimate more accurately the number of differentiated evolutionary units (Cracraft, 1983a).

The results are shown in Table 2. Diversity in both families parallels the gradient in lithospheric complexity. It is also noteworthy that this is especially true even when area is taken into account; diversity is not related to a simple area-effect. Amazonia covers a much greater area, yet contains only about the same number of differentiated taxa within these two families as does Central America. Also revealing is the number of taxa per genus that have differentiated in the three areas. For both families, the Andean region shows the greatest average amount of differentiation per genus, followed by Central America, and then Amazonia.

OTHER RATE-CONTROLS OF SPECIATION

Spatial and temporal variation in lithospheric complexity has been hypothesized above to effect a major control on speciation rates, and thus to contribute significantly to explaining patterns of diversification. Other factors are also widely acknowledged to contribute to variation in speciation rates, and the purpose of this section is to assess their contribution. Not all the evidence for and against these factors will be reviewed here—their existence and potential importance is assumed. Instead, this discussion evaluates whether they might constitute a significant causal mechanism underlying patterns of diversification. It will be argued that, although these factors might influence speciation rates within clades (and in some cases perhaps significantly so), they appear to have had a limited impact on defining major spatial patterns of diversity.

INTERNAL MORPHOGENETIC COMPLEXITY

Differentiation following isolation is a function of the amount of morphogenetic complexity

within the individuals of a species. If those individuals exhibit little or no variation, then the rate-change in character divergence following isolation should be low, and thus too the probability of differentiation (Stanley, 1975, 1977; Wiley & Brooks, 1982). Morphogenetic complexity means the amount of variation as expressed within the developmental pathways of individuals of a population, a notion equivalent to the concept of canalized information as used by Wiley and Brooks (1982). Any changes within the genome that have effects on developmental pathways, and thus on phenotypic expression, are potentially important in establishing the probability that a population will differentiate once it becomes isolated. Thus, variation in morphogenetic complexity within the species of a clade might influence their speciation rate (Cracraft, 1982a): clades comprised of species having high internal complexity should speciate at a higher average rate than clades with less complex species (all things being equal).

Present evidence suggests, for example, that genomic modifications such as gene duplication, polyploidy, and gene rearrangements, in addition to point mutations, can alter developmental pathways and thus adult phenotypes (Wilson et al., 1977). As a consequence, the prediction might be made that if individuals within a clade are characterized by these types of genomic modifications, then the probability of speciation will be relatively high. Wilson et al. (1977), in fact, proposed that speciation rates in mammals have been higher than those for anurans partially because of a higher rate of chromosomal change in the former. Levin and Wilson (1976) made a comparable claim to explain patterns of diversity within angiosperms.

Properly designed comparative studies should give us much more insight into the causal relationship between large-scale genomic change and speciation rates within and among clades. If this relationship proves significant, the question will arise as to how that might be relevant at the level of diversity gradients within biotas. At first glance, it might appear difficult to conceive of numerous clades exhibiting congruent patterns of genomic modification among their species, yet such geographic gradients have been suspected for some time. The incidence of polyploidy, for instance, increases with increasing latitude (Grant, 1971); what effect that has had on geographic variation in speciation rates is a separate, as yet unanswered, question.

BEHAVIORAL-ECOLOGICAL ATTRIBUTES OF SPECIES

Biologists have long hypothesized a causal connection between certain behavioral-ecological attributes of species and the likelihood that they might speciate. Unfortunately, conflicting predictions or expectations are common. Substantial literature suggests that ecological generalists (or eurytopes) would be more likely to colonize distant habitats, become isolated, and differentiate, than would specialists, or stenotopes (see Parsons, 1983 for a summary; also Kohn, 1971; MacArthur, 1972; Diamond, 1975, among many others). Yet, stenotopy, rather than eurytopy, has been hypothesized to lead to speciation through small, ecologically restricted populations (Jackson, 1974; Eldredge & Cracraft, 1980; Vrba, 1980, 1983). The best available data supporting this latter hypothesis are those of Jablonski (1982; see also Valentine & Jablonski, 1983), in which gastropods and brachiopods with nonplanktotrophic larvae (stenotopes) presumably speciate at higher rates than those with planktotrophic larvae (eurytopes).

While it seems clear that possession of certain ecological or behavioral characteristics may help determine the probability of speciation for species within a clade, this can translate into geographic patterns of diversity only if the characteristics themselves vary geographically, if they vary in the right direction, and if the different clades of organisms comprising the biota being investigated show covarying sets of characteristics when displayed geographically. Such a conjunction of events suggests this would occur only very rarely, and consequently this category of speciation rate-control probably has little influence on geographic diversity gradients.

SEXUAL SELECTION

Fisher (1930) proposed that a genetic correlation between assortative mating created by female choice, on the one hand, and secondary sexual characteristics of males (the basis for the choice), on the other, can lead to rapid evolutionary change within populations. Lande (1981, 1982) and West-Eberhard (1983) have also argued that such "runaway" sexual selection might be responsible for high rates of speciation in some groups.

In theory, this mechanism for rapid divergence might be potentially important in those groups of organisms possessing the appropriate mating

systems (West-Eberhard, 1983). Yet, an upper-level constraint on this process of divergence would still exist and include those factors controlling the rate of geographic isolation; in most cases, sexual selection itself could influence the rate of divergence only after populations became isolated.

The influence of sexual selection on speciation rate thus remains highly speculative. Unless the incidence of sexual selection varies geographically—e.g., if sexual selection were more frequent in highly diverse ecosystems (as perhaps is the case)—then its contribution to establishing geographic gradients in diversity would be minimal. Even if this geographic variation existed, however, speciation would not be expected to occur faster than the rate of geographic isolation.

The Rate-Control of Extinction

Despite a large literature, biology still lacks a widely accepted deterministic theory of extinction. Emphasis has been placed on the occurrence and explanation of short-term pulses (so called "mass" extinctions) rather than on the patterns and processes of normal "background" extinction. Another factor mitigating against the development of a theory of extinction has been the difficulty of testing any proposed hypothesis. The analysis of causation within extinction theory is particularly susceptible to scale effects: at one level climate may change, thereby initiating numerous environmental consequences leading to extinction, but at the same time that extinction also can be examined causally at the more "proximate" level of processes within populations.

At issue here are patterns of extinction calling for explanations at hierarchical levels above that of populations. Such patterns are taxonomic, at the level of clades, and biotic, at the level of assemblages of species, or some combination of both. Thus, taxonomic patterns of extinction within or among clades can be expressed either geographically or temporally at a single location. Patterns of extinction within biotas are statistical summations of extinction within and among clades. Within a biota, changes in extinction rate are expressed temporally, whereas patterns between biotas can be both temporal and geographic.

These large-scale patterns, above the level of populations, can be expected to have first-order causes which themselves are expressed at a hierarchical level above that of populations. It is proposed here that change in the temporal and geographic gradient of environmental harshness (favorableness) is the primary control of extinction rates, and thus of the large-scale extinction patterns just mentioned. This hypothesis will be developed in more detail now and later will be compared with other potential rate-controls of extinction.

THE HYPOTHESIS OF ENVIRONMENTAL HARSHNESS

The twin concepts of environmental harshness and favorableness have been discussed extensively in the ecological literature (especially Andrewartha & Birch, 1954). Most of that literature relates harshness with density-independent population regulation (see Enright, 1976 for a discussion of how harshness might function within a density-dependent context). The hypothesis presented here expands that thinking to account for large-scale gradients in extinction.

Premise 1. Individual organisms (and thus populations and species) possess a definable physiological capacity permitting them to exist within a specific environmental regime; no organism or species can live in all environments.

Premise 2. As the physical characteristics of an environment shift away from the "optimal" conditions for a species, the intrinsic rate of increase declines and eventually becomes negative, resulting in extinction of the population.

In this case, we define "optimal" in terms of the conditions (narrow or broad) at which the rate of increase is at or near maximum, but other measures could also be chosen. This premise has considerable empirical support, and physical attributes of the environment are known to influence physiological functions, which in turn have effects on demographic parameters such as fecundity, survivorship, age of reproduction, among others (Andrewartha & Birch, 1954; Ricklefs, 1973; Krebs, 1978).

Premise 3. The environments of the earth can be arranged along a scale defined in terms of their harshness/favorableness relative to the mean physiological tolerances of a random sample of the world's organisms.

Many physical parameters have the potential to influence the survivorship and reproductive capabilities of organisms. Moisture and temperature gradients are generally acknowledged to exert a greater overall effect than do other parameters, and that assumption is adopted here. Therefore, the premise states that, in principle,

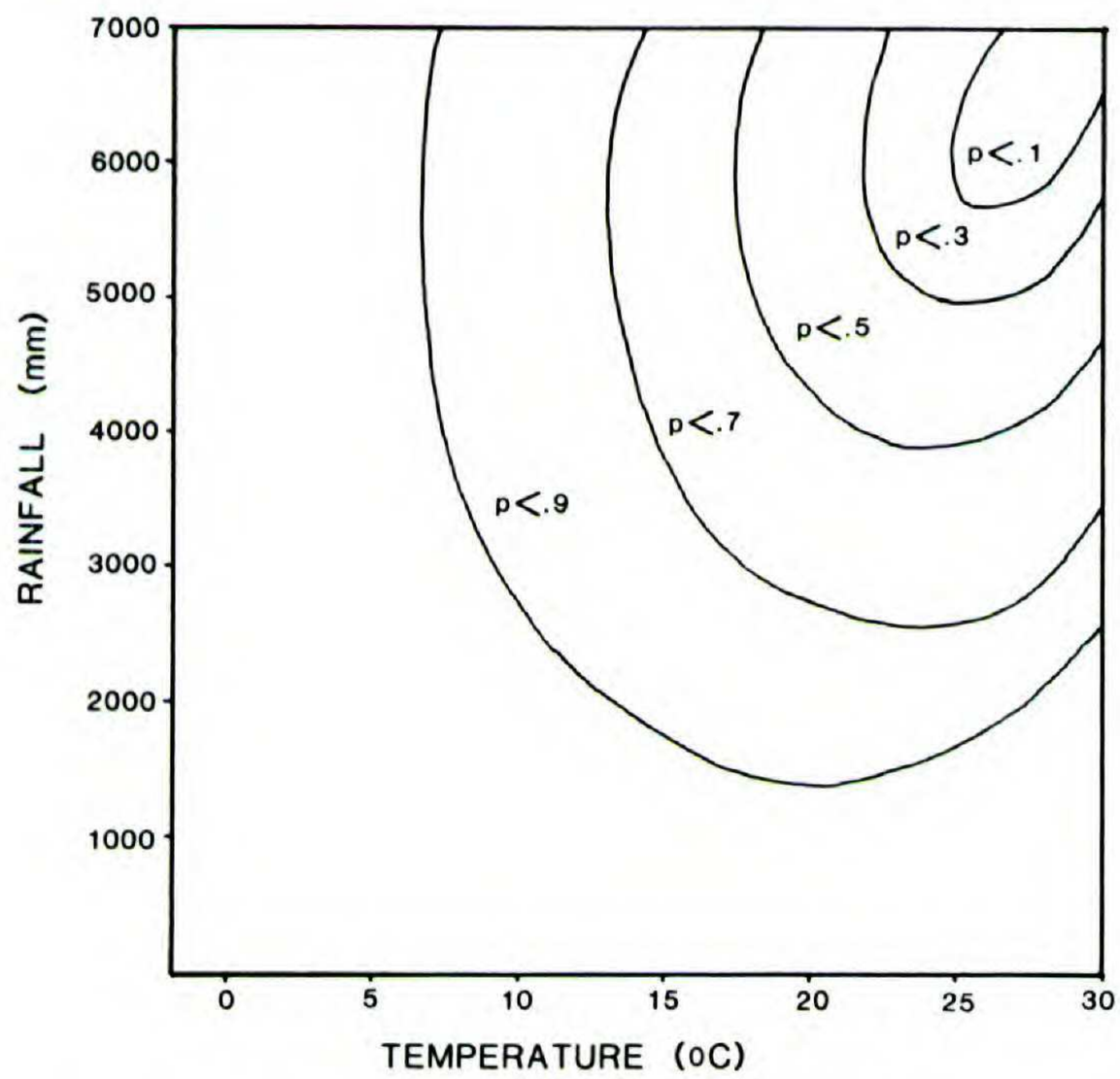

FIGURE 6. A theoretical diagram postulating a relationship between the probability of extinction and the position of a population in a space of environmental harshness/favorableness, as measured in terms of mean annual rainfall and temperature (modified after Birch, 1953 and Krebs, 1978).

the joint influences of temperature and moisture on the intrinsic rate of natural increase can be experimentally determined for each species (e.g., the classic study of Birch, 1953), and a measure of that influence (harshness/favorableness) can be mapped geographically.

Premise 4. The frequency of species occurrences along the harshness/favorableness scale is decidedly nonrandom.

Also having much empirical support, this premise merely states that environmental extremes in temperature and/or moisture are tolerated by relatively few organisms. In areas of low harshness (generally speaking, in environments that are warm and moist; see below), organisms require less energy to maintain physiological homeostasis relative to their surroundings than do organisms in harsher environments.

These premises yield the following hypothesis: *the probability of extinction is a function of the change in the value of environmental harshness to which a species is exposed* (Fig. 6).

The hypothesis makes more explicit what biologists have intuitively recognized for many years. But it also makes a larger claim not often recognized: that taxonomic and biotic patterns of extinction are *primarily* a function of spatiotemporal changes in environmental harshness. Ecologists have long proposed a relationship between environmental harshness/favorableness and diversity (e.g., Richerson & Lum, 1980), but most of these discussions have not pinpointed the causal connection of this relationship: that is, harshness influences only *one* component of diversification, namely extinction rate (see Connell, 1975 for a discussion of the ways in which harshness gradients influence community structure).

Extinction rates are exceedingly difficult to study because their analysis is more dependent on the quality of the fossil record than is the analysis of speciation rates. For example, if we compare Recent sister-clades differing greatly in diversity, the minimal number of speciation events for each clade can be specified (N-1, where N is the number of species) even in the absence of a fossil record; relative rates can thus be estimated directly. On the other hand, a comparable statement regarding the number of extinctions in each lineage is not possible in the absence of a fossil record. A method must be found to document the loss of a species, not its mere presence, and a historical record is our only way of doing this.

Measurements of extinction rates based upon an analysis of the fossil record entail additional difficulties in that paleontologists rarely use species-level taxa but often are compelled instead to study taxa at the generic or family levels, precisely because of the lack of detail in the fossil record. Unless the supraspecific taxa contain the same average number of species (and with little variance), however, comparisons among them will not yield accurate statements about the relative amounts of extinction at the relevant evolutionary level, namely that of species.

Evaluation of the hypothesis of environmental harshness not only relies upon the fossil record for an estimation of relative rates of extinction, but also for the measurement of changes in harshness through time. The components of harshness, here considered to be temperature and moisture, are retrievable from both paleontological data and from physical and chemical characteristics of the rock record itself. Unfortunately, detailed study of the relationship between extinction rate and harshness calls for a well-preserved historical record, which is usually lacking for terrestrial environments. Despite its inadequacies, paleontology can provide, nevertheless, abundant data at a coarse-grained level with which to evaluate the hypothesis of environmental harshness.

A major prediction of this hypothesis is that as a specific environment becomes harsher, the average extinction rate of the component species of the biota will rise. As defined earlier, harshness increases as temperatures and moisture approach extreme values. Under these conditions, more organisms become physiologically stressed, population sizes decline, and the probability of extinction increases. Paleontologists have documented numerous cases of increases in extinction rates accompanying climatic shifts toward harsher environments (Axelrod, 1967). For example, the marked increase in elevation of the Andes in the middle to late Cenozoic resulted in a change toward extreme aridification along the west coast of South America, thereby causing a once diverse biota to become extinct and be replaced by one much less so (Berry, 1938). A widespread, relatively diverse biota disappeared in North Africa as the climate became more arid in the late Cenozoic (Moreau, 1952, 1966). Similar changes in moisture and extinction gradients also took place in Australia (Kemp, 1981; Galloway & Kemp, 1981).

Increases in harshness as measured by temperature are also known to have increased extinction rates. Hickey (1981, 1984) reported a gradual increase in the extinction rates of floras as global temperatures became cooler across the Cretaceous-Tertiary boundary. Furthermore, extinction rates were higher in higher latitudes where the temperature gradient was steeper. That deviations in temperature away from physiologically more favorable regimes increase extinction rates of floras has been noted by many workers, and perhaps the classic example is that associated with the Pleistocene climate fluctuations (e.g., Axelrod, 1967; Kershaw, 1981). Finally, in the marine realm, temperature change is also strongly implicated in large-scale extinction events (Stanley, 1984; Kauffman, 1984).

That large-scale, geographic increases in environmental harshness result in concomitant responses in the steepness of extinction gradients can scarcely be denied, yet this does not inform us about the relative role of increased harshness, when compared to other postulated causes of extinction, in effecting a control over patterns of diversification. At the level of biotas, changes in harshness seem to play an important part in the evolution of geographic patterns of diversity, but their relative contribution to controlling patterns of diversity, within and among clades is somewhat more difficult to establish because a relatively extensive fossil record is required. Most clades are distributed nonrandomly and so global changes in harshness should alter extinction rates of clades nonrandomly (e.g., as in latitudinal gradients). Changes in harshness, however, often result from relatively local tectonic evolution, and thus patterns of extinction within clades might exhibit a "stochastic" appearance over a large geographic area (i.e., clades would go extinct, in this case, purely as a result of being in the wrong place at the wrong time).

Many clades show a pattern of reduction diversity during their history, but the causes of this common pattern have not yet been analyzed comparatively. Unfortunately, it is not possible at this time to evaluate the generality of the environmental harshness hypothesis by reference to a large suite of phylogenetically controlled data. As an alternative, we can undertake a partial evaluation by examining other postulated causes of extinction and assessing their potential for explaining both intracladal and geographic patterns of biotic diversity.

a. *Tectonic elimination of habitats.* Tectonic activity brought about by lithospheric plate motion directly obliterates habitats (e.g., shallow and deep-water marine environments during continent–continent collisions) or changes in their extent through mountain building, alterations in sea-level, or volcanism (Valentine & Moores, 1970, 1972; Valentine, 1971, 1973; Schopf, 1974; Bakker, 1977; Hallam, 1981; Axelrod, 1981). Tectonic events can have major effects on the extinction patterns of local biotas, and generally are recognized to contribute to mass extinctions. In particular, if these events have a large geographic scale, then they can alter patterns of diversity within higher taxa (examples can be found among the major Phanerozoic mass extinction events). Whether tectonic events are a major, direct control on long-term patterns of reduction diversity within clades is questionable, although marine regressions and transgressions can span many millions of years and might alter diversity gradually.

Tectonic activity per se is thus not likely to be the principal causal agent of most geographic gradients in extinction or of long-term patterns of reduction diversity (particularly within terrestrial organisms). But tectonic alterations of environments play a significant role in geologically "short-term" mass extinctions, and thereby could leave their signature on "long-term" patterns of diversity within clades. The extent to which these

geological events could help explain congruent changes in diversity over many clades would depend upon the magnitude of the events themselves, their location, and the clades of organisms that happen to be exposed to them.

b. *Competition.* Ecologists have long identified competition as a major cause of extinction within populations, and the tradition goes back to Darwin himself. Paleontologists and others interested in large-scale patterns of diversification have adopted many ecological ideas regarding competition and its role in extinction and have reified them as patterns and processes among higher taxa. A common application of this thinking occurs when one group of organisms is said to "replace" another, trophically similar group over a period of time (perhaps many millions of years). Well-known examples ascribed to competition include the replacement of creodonts by condylarths (Simpson, 1953), South American marsupials by North American placentals (Simpson, 1950), multituberculates by primitive placentals (Simpson, 1953; Van Valen & Sloan, 1966), dinosaurs by placental mammals (Van Valen & Sloan, 1977), and even invertebrates by primitive gnathostome fishes (Thomson, 1977), to name only a few. If the causal assessment of these replacements is correct, then by implication competition would be a major factor leading to reduction diversity within clades.

None of these putative examples is well documented, however, at least by the standards currently acceptable within modern ecology (Wiens, 1977; Connell, 1975, 1980, 1983). Many difficulties arise, first in recognizing the mere presence of competition within Recent communities, and then, second, in determining that it is an important force controlling the relative abundances of species within those communities. To extend this type of analysis to fossil communities magnifies these difficulties to a point at which the problems become intractable. Showing that one species competitively replaces another requires extensive ecological analysis; arguing that many species of one clade (or one biota) can competitively replace many species of another clade or biota requires detailed data that a fossil record is incapable of supplying. The "replacement" can be documented, but a causal hypothesis of competition cannot.

The proposition that competition is a major factor controlling extinction rates and thus shaping patterns of diversity is unsupported. We could reach this conclusion, moreover, *even accepting* the hypothesis that competition is ubiquitous and important in the regulation of species abundances within local communities. But given that this latter hypothesis is still being debated within ecology, it seems premature, and perhaps presumptive, to conclude that competition is a major causative agent of extinction either within clades or between biotas (see Gould & Calloway, 1980, for an analysis of the "classic" brachiopod-to-clam replacement, which they conclude resulted from the Permian extinction event not competition).

c. *Predation.* Predation is postulated to be an important factor in regulating relative abundances within populations. Depending upon the ecological system being studied, the presence and effect of predation may or may not be easily determined. Within paleontological assemblages, predation has been investigated most extensively in marine invertebrates in which evidence is often obtained directly from the fossils themselves. These studies suggest the possibility that predation pressure has increased the extinction rates in some clades or organisms. Stanley (1977), for example, postulated that the post-Paleozoic increase in the frequency of shelled infaunal bivalves as compared to exposed epifaunal forms was the result of more intense predation on the latter. This "species selection," Stanley (1977: 238) proposed, led to higher extinction rates of epifaunal species and major changes in diversity within and between clades. Likewise, Stanley (1977) attributed the post-Late Mesozoic decline of articulate brachiopods to increased predation from teleost fish, snails, and crabs.

The significance of predation within ecosystems cannot be denied, yet acceptance of its importance as a causal agent controlling rates of extinction is less warranted. Under most natural conditions, predators do not extirpate their prey, although at times they may affect their numbers substantially. If predation does not cause extinction of a prey species directly, population sizes might be so reduced that extinction could occur stochastically or via other agents. Predation might be expected to play a role in species extinction in communities with simple structure in which prey species cannot (or have failed to) develop any effective means of predator avoidance. In contrast, if prey species are widely distributed or have high dispersal abilities (or are unavailable to predators) during some part of the life cycle, then the probability of extinction via predation would be expected to be relatively low.

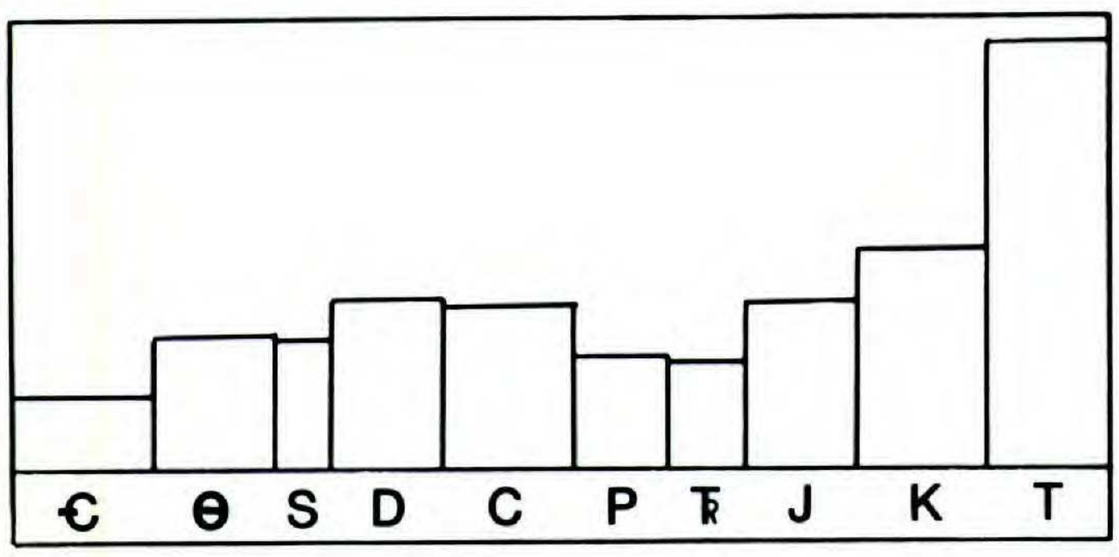

FIGURE 7. Phanerozoic species diversity curve for marine invertebrates showing a marked rise in diversity in the Cretaceous and Tertiary (after Raup, 1976a and Sepkoski et al., 1981).

As a consequence of these factors, predation will probably not be an effective mediator of extinction rates in most groups of organisms. Any hypothesis that predation is important needs to be critically evaluated and thoroughly documented.

d. *Behavioral characteristics.* The degree of behavioral-ecological plasticity of species has been postulated to influence the probability of extinction. Jackson (1974), Eldredge (1979), Eldredge and Cracraft (1980), and Vrba (1980) have suggested that eurytopic species will be less likely to go extinct than stenotopes. Eurytopic species tolerate a relatively wider range of environments, and are thus assumed to be more widely distributed and have larger overall population sizes than stenotopes. Extinction rates are postulated to be higher in stenotopes because of their smaller, more narrowly distributed populations.

The correlations (e.g., Vrba, 1980) between eurytopy and clades of low diversity, and between stenotopy and clades of higher diversity, are not easily interpreted. Stenotopic species presumably have higher probabilities of both extinction and speciation; in such cases, therefore, high speciation rates would be postulated to override high extinction rates. Eurytopic species, in contrast, are assumed to be characterized by both low extinction and low speciation rates. If eurytopic clades are generally characterized by low diversity, then that would probably result from the low speciation rates and not low extinction rates, which should instead promote high diversity. Consequently, this suggests that stenotopy and eurytopy, to the extent that they influence intracladal diversity, do so through the mediation of speciation rates and not through effects on extinction.

The preceding discussion makes clear the complex causation underlying extinction rate-controls. Any temporal change in diversity that is attributable to extinction rather than speciation almost certainly will be a manifestation of different causal processes operating simultaneously. Accepting this, we should seek to identify the relative contributions of each cause to the extent possible. In most cases, the available data probably will not permit us to discriminate much more than one or two main factors.

The evidence reviewed here suggests that intracladal patterns of reduction diversity and geographic gradients of diversity, insofar as they reflect variation in extinction, are generally the result of gradients in environmental harshness. This claim is merely one of frequency. Many kinds of tectonic activity can alter extinction rates of biotas on a local scale or sometimes even over areas of considerable extent. Behavioral attributes such as eurytopy and stenotopy have the potential to influence extinction rates, although because they can also affect speciation rates, their analysis is complicated and their role in extinction is questionable. In principle, competition and predation, through their effects on species abundances, might contribute to regulating the probability of extinction but, once again, the analysis of this contribution is exceedingly difficult, if not impossible, in most situations. Moreover, even though populations might be subject to these presumed density-dependent interactions, density-independent factors might actually be the primary controls on mortality (Enright, 1976). The conclusion is that only environmental harshness is likely to constitute a significant influence on the types of extinction patterns considered here. Because of its pervasive, and well-documented, influence on extinction, the effects of environmental harshness should be eliminated prior to considering other causal hypotheses. Such a procedure will ensure that those hypotheses are evaluated under the best possible circumstances.

DISCUSSION

WHAT IS THE SHAPE OF THE PHANEROZOIC DIVERSITY CURVE?

The Phanerozoic diversity curve has been the subject of much discussion over the past decade (Valentine, 1972; Raup, 1972, 1976a, 1976b; Bambach, 1977; Sepkoski, 1978, 1979; Sepkoski et al., 1981; Signor, 1982). Arguments have centered on the empirical shape of the curve itself, in particular whether diversity has been at equilibrium since the end of the Paleozoic or whether

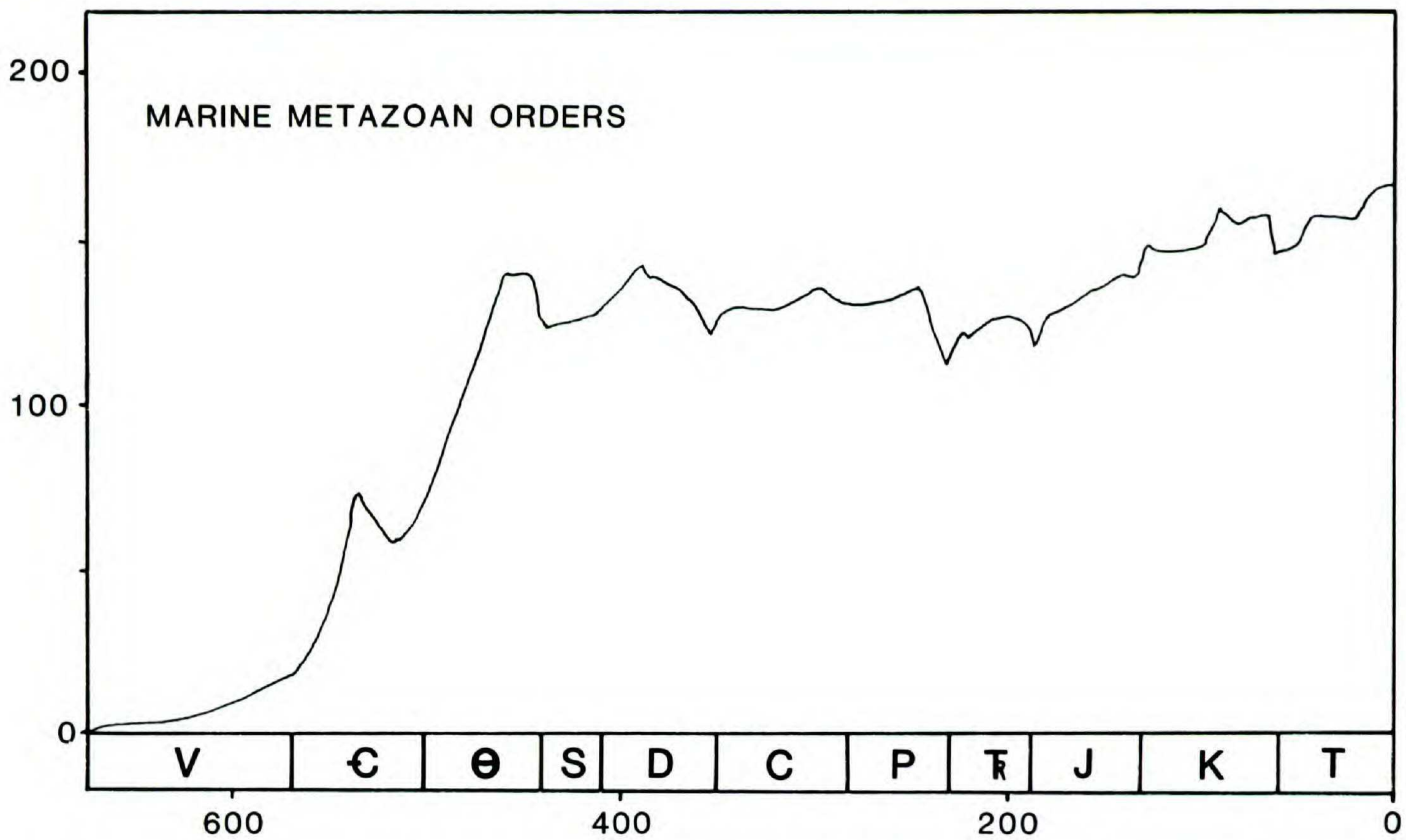

FIGURE 8. A Phanerozoic diversity curve for marine "orders" of Metazoans (from Sepkoski, 1978). Curves such as this have been used to support the hypothesis that diversity has been in equilibrium since the late Paleozoic.

there was a late Mesozoic-Cenozoic rise. Various authorities now generally agree that present data show a curve for marine invertebrates that rises abruptly from a Cambrian low to one of apparent equilibrium through the Permian, followed by a dip in the Triassic, and a subsequent increase in the late Mesozoic and Cenozoic to levels that were four to eight times those of the Paleozoic and early Mesozoic (Sepkoski et al., 1981; Signor, 1982; Fig. 7).

Our concern here is not with the actual empirical shape of the curve but with its expected shape given specific models of diversification. With respect to the former, one might argue that available data, which are primarily of marine organisms, are inadequate to test any of the curves that might be predicted. For one thing, a meaningful evaluation of the pattern of diversification cannot be restricted solely to marine taxa (e.g., Sepkoski et al., 1981), because many of them also have radiated into nonmarine environments. Consequently, although the marine pattern is of interest in its own right, most workers would probably agree that it cannot be the benchmark of the Phanerozoic curve itself. Restriction of an analysis to one biotic association (marine, arboreal, terrestrial, freshwater) is only a partial sample of the results of diversification; none of these ecological subdivisions is a closed system as far as diversification is concerned.

Furthermore, estimations of the shape of the diversity curve based on counting supraspecific taxa are inherently biased and inaccurate (Cracraft, 1981b, 1982a; Novacek & Norell, 1982; and earlier discussion). Higher taxa are not equivalent in terms of age, nor does a temporal comparison of their numbers necessarily reflect an accurate comparison of the numbers of evolutionary units within those taxa.

Finally, the Phanerozoic record for freshwater and terrestrial environments is much too poor to provide an accurate estimate of the numbers of species from one time period to the next. As a simple example, the estimated number of *living* arthropods increased tenfold (to perhaps 30–40 million species) in the last few years after it was realized just how diverse the tropical forest canopy is (T. L. Erwin, 1982; pers. comm.). Tropical invertebrate faunas, in general, are still virtually unknown. Given the fact that the most highly diverse biotas (i.e., those that are tropical) are amongst the most poorly preserved in the fossil record, accurate estimates of diversity based on that record should not be expected.

To summarize, we can only praise the efforts of those who have attempted the arduous task

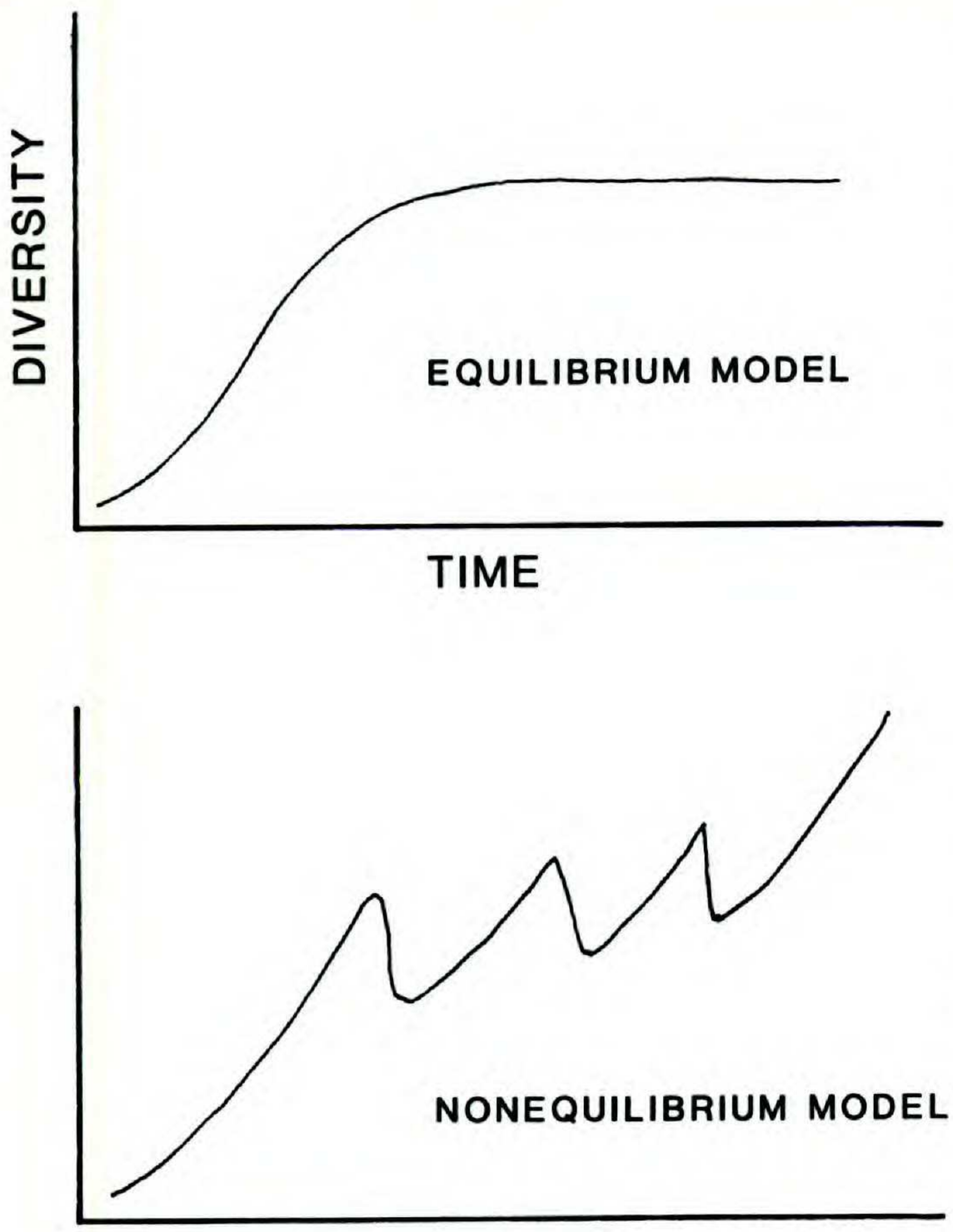

FIGURE 9.—A. Curve illustrating the equilibrium model of biotic diversification. Perturbations such as mass extinctions depress the curve temporarily but diversity eventually rebounds to or near the equilibrium level.—B. A nonequilibrium model of biotic diversification. An intrinsic exponential increase in diversity is expected with the rate of increase constrained by worldwide patterns of environmental harshness/favorableness. Major perturbations such as mass extinctions are postulated to "reset" the curve (see text).

of compiling patterns of diversity from the fossil record, and their emphasis on the marine fossil record is readily understandable. The message here is merely that some skepticism is necessary regarding what these curves actually tell us. They may reveal an accurate picture of diversification patterns within the marine realm itself, yet clearly that record does not depict actual patterns of diversification of all those clades within the biosphere as a whole.

Consequently, the question can be asked: what might be the expected shape of the Phanerozoic diversity curve? Investigators of marine diversity have often assumed the marine environment to be a closed (or semi-closed) system, and the diversity curve therefore to be logistic, or equilibrial (Sepkoski, 1978, 1979; Figs. 8, 9A). Within such a system, perturbations such as mass extinctions depress the curve, but diversity eventually rebounds to the equilibrial value. Only minor variation above equilibrial values would be expected.

If diversification is controlled significantly by lithospheric evolution, isolate formation would be some exponential function of the rate of barrier formation (Cracraft, in prep.). Diversity, therefore, would increase through time. But the path of the diversity curve is constrained by extinction, including both mass and the background rate. In this model, mass extinctions "reset" the curve of diversification, not perturb it from an equilibrial value (Fig. 9B), and changes in the background rate of extinction—as would occur, for example, during periods of global cooling or warming—operate to calibrate the exponential rise function.

Ecologically, a diversity-independent diversification model would not entail a saturation of the resource-space of the biosphere. Indeed, in the absence of external constraints (extinction), that space should grow through time. When differentiation produces new species, it also produces taxa having new (or modified) ways of utilizing the physical and biotic space of the biosphere. Because different trophic levels of a biota have different relative abundances, repeated vicariance of that biota might be expected to yield different diversification rates within each trophic level: we would predict, for example, that the primary consumer (herbivore) level would increase at a higher rate than the secondary consumer (carnivore) level. This may explain the inordinately high numbers of herbivores in systems that have experienced relatively few extinction events over time (e.g., terrestrial environments in the tropics as compared to temperate regions; see below).

Empirically, the Phanerozoic diversity curve seems to fit the diversity-independent model more closely than an equilibrial model. Sepkoski et al. (1981) and Signor (1982) document a precipitous rise in marine diversity since the Triassic, exactly what might be expected given the absence of a major mass extinction during that time (only two "intermediate" events are recorded in the marine record; Sepkoski, 1982). Because this rise is so far above the Paleozoic "equilibrium" level, an equilibrial model cannot easily explain it, whereas the diversity-independent model can.

The hypothesis that Phanerozoic diversity was at some equilibrial value from the Ordovician to the end of the Permian (almost 250 Ma) is also open to challenge and to the claim that di-

versification could have been nonequilibrial (Ross, 1972). First, two significant extinction events, the Ashgillian in the late Ordovician and the Frasnian in the middle to late Devonian (Raup & Sepkoski, 1982), can be hypothesized to have "reset" the diversification curve of the marine biota of the time. Second, although marine diversity appears reasonably constant from the Carboniferous until the end of the Permian, many other groups were apparently radiating into terrestrial and freshwater environments at that time: e.g., amphibians (Carroll, 1977), conifers (Florin, 1951). These groups are underrepresented in calculations of the Phanerozoic species diversity curve.

Finally, the Permo-Carboniferous was a period of harsh global climates (Frakes et al., 1975; Olson & Vaughn, 1970), which can be postulated to have constrained diversification. If true, then the expected exponential rise might have been "damped," thus contributing to the appearance of a diversity equilibrium.

Insufficient evidence thus exists to conclude that Phanerozoic diversity has exhibited an overall pattern of equilibrium. Moreover, there is little reason to expect that speciation and extinction are diversity-dependent (Cracraft, in prep.). The expectation of equilibrium, which has been so widely accepted within the paleontological community, has arisen from an acceptance of only one view within contemporary ecology regarding population regulation and from the assumption that processes at the hierarchical level of clades and biotas are simple extrapolations of ecological processes within and between populations. As these latter processes do not appear to constitute first-order determinants of speciation or extinction, that extrapolation is probably not valid.

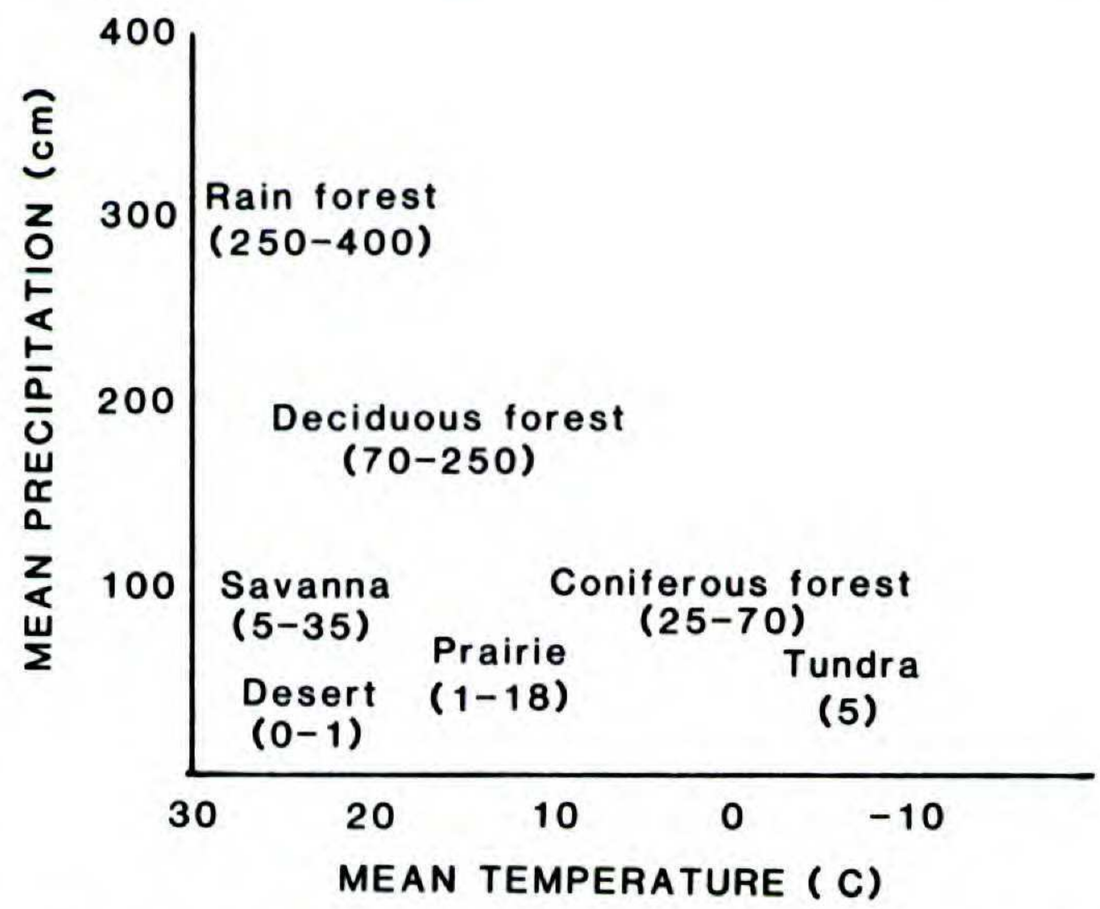

FIGURE 10. Biomass production (tons/hectare) of different vegetational associations relative to a gradient in environmental harshness/favorableness, as measured by mean annual temperature and precipitation (after Smith, 1980). Potential biomass production is constrained by worldwide patterns of environmental harshness (see text).

IS THERE AN UPPER LIMIT TO DIVERSITY?

Acceptance of the idea that biomass has attained an equilibrial value within the biosphere has been the basis for concluding there exists an upper limit to diversity (MacArthur, 1965, 1969; Margalef, 1972; Levinton, 1979). The previous discussion, however, has questioned the underlying assumption of a limit to the evolution of biomass, and that viewpoint will be amplified here (see also Benton, 1979; Cracraft, in prep.).

As long as the biosphere is an open thermodynamic system (Ulanowicz, 1980), the influx of energy and matter will continue to be captured by organisms, ultimately through the processes of reproduction and ontogeny, with biomass thus increasing. Degradation of the earth by chemical and physical processes, and also by organisms, releases matter, some of which is incorporated into living organisms. Incoming solar energy is transduced and used to manufacture organic material, yet only a very small portion (1% or less; Krebs, 1978: 522–524) of the available energy is utilized. Given these observations, then, an increase in biomass would appear to be inevitable, unless some extrinsic factor can be shown to constrain the flow of energy and matter.

Ecologists have often viewed the evolution of biomass and diversity as being tightly coupled so that there is an inverse relationship between diversity and relative abundance. In a biomass-limited world, such an assumption is logically compelling. Still, the evolution of diversity could be related to the evolution of biomass in yet another way. The flux of energy and matter through individuals and populations is the motive force for ontogenetic and evolutionary differentiation (Wiley & Brooks, 1982; Brooks & Wiley, 1984). Thus, diversification takes place as a consequence of biomass expansion. Moreover, as long as energy flow through the lithosphere continues to drive its evolution, taxonomic differentiation will persist unabated.

But are there no limits to biomass evolution? Biologically more meaningful, perhaps, is to speak of constraints on biomass evolution within the

context of a nonequilibrium increase (Ulanowicz, 1980). Through the history of life the most important constraint has probably been a steep gradient in environmental harshness. On the earth today, for example, climates of harsh temperature and moisture regimes restrict net primary productivity (Fig. 10). This observation also implies that space itself has not been a limiting factor of global biomass production. At any one location, however, biomass production could be limited by a variety of factors, abiotic or biotic.

ECOLOGICAL EXPLANATIONS AND THE ANALYSIS OF LARGE-SCALE DIVERSITY GRADIENTS

Ecologists have long played a leading role in the analysis of diversity, particularly since Hutchinson's (1959) seminal paper. These efforts have been directed primarily toward the solution of two questions: (a) How can latitudinal gradients in diversity be explained? and (b) How can variation in diversity among different habitats be explained? By and large ecologists have considered the answer to the first question to be an extension of the answer to the second. The discussion that follows takes the approach that the answers to the two questions are largely independent—that is, neither is a logical or biological corollary of the other.

Ecological approaches to diversity have been extensively reviewed by others (Connell & Orias, 1964; MacArthur, 1965; Pianka, 1966; Whittaker, 1972, 1977; Ricklefs, 1973; Rosen, 1981; Thiery, 1982), and although each categorizes potential explanations somewhat differently, a common list can be generated.

Explanation 1. The *time-stability hypothesis* states that the longer a community has maintained stability and not been subject to major disturbance (extinction), the more species will accumulate.

Explanation 2. The *spatial heterogeneity hypothesis* predicts more species will co-exist in environments that are more complex spatially. As Pianka (1966: 36–37) noted, the concept of spatial heterogeneity is also a problem of scale, and ecologists, more often than not, refer to local within- or between-habitat complexity when comparing differences in diversity (MacArthur et al., 1962, 1966; MacArthur, 1964; Ricklefs, 1977).

Explanation 3. The *productivity hypothesis* states that as environments increase in productivity, diversity will increase (Connell & Orias, 1964).

Explanation 4. The *competition hypothesis* argues that as competition increases, organisms become more specialized and niche sizes decrease, and hence diversity can increase (MacArthur, 1965, 1972). A variant of this hypothesis states that the evolutionary impetus to reduce competition results in more niche overlap and thus higher species diversity (Klopfer & MacArthur, 1961).

Explanation 5. The *predation hypothesis* states that as predators increase in numbers, they reduce population sizes of their prey, thus allowing more of those species to coexist (Paine, 1966; Janzen, 1970).

Ecologists have been quick to point out that no single hypothesis can explain spatial gradients in diversity, and consequently some combination of the above five explanations is generally invoked (Pianka, 1966; Menge & Sutherland, 1976; Huston, 1979). Yet even this misses the point because supporters of these hypotheses rarely address the question of the rate-control of speciation and extinction (Ricklefs, 1973 is an exception), which, it has been argued, is the first-order cause of large-scale diversity gradients.

Ecological explanations have generally confounded two issues: the generation of diversity versus its maintenance. By and large, ecologists have spoken only to the latter, and thus a causal relationship between their explanations and the underlying determinants of diversity—speciation and extinction—usually is not addressed. Ricklefs' (1973: 714) classification of diversity hypotheses is one attempt to do this, but that effort primarily functions to expose the inconsistencies among some of these hypotheses. For example, competition is said to be more intense in tropical situations, thus increasing natural selection and thereby leading to faster evolution (Dobzhansky, 1950). Yet at the same time, competition is claimed to be *less* stringent in the tropics, thus leading to lower extinction rates (Ricklefs, 1973: 714, table 43-5). Likewise, greater "productivity" is hypothesized to lead to greater turnover of populations, thus increased natural selection, and faster evolutionary (speciation) rates; in contrast, more "resources" also are said to result in less competition, thus damping natural selection and thereby lowering extinction rates.

The hypothesis advanced here is that these presumed ecological correlates of high diversity,

rather than being causes, are simply *effects* of having more species together in the same place. None of them is sufficient to account, in any regular manner, for the spatial gradients of speciation and extinction rates that are necessary to produce observed patterns of diversity. In contrast, these ecological correlates can be explained as consequences of those same gradients. Thus, higher productivity, narrower niches, more niche overlap, more competition, more predation, and more habitat heterogeneity might be expected in communities having relatively more species.

DEEP-SEA DIVERSITY AND TIME-STABILITY HYPOTHESIS

One of the most intriguing spatial gradients of diversity is the increase of the deep-sea benthos relative to the continental shelf and abyssal plain (Hessler & Sanders, 1967; Sanders, 1968; Rex, 1981a, 1981b; see Fig. 4). Although this increase has been explained as an effect of area and thus not requiring a separate deterministic explanation (Abele & Walters, 1979a, 1979b), Rex (1981a) reanalyzed available data and concluded that the additional diversity on the continental slope and rise is not area dependent.

Explanations for the parabolic shape of the deep-sea diversity gradient (Fig. 4) have been ecological, and the time-stability hypothesis has been particularly influential (Grassle & Sanders, 1973; Hessler & Sanders, 1967; Sanders, 1968, 1969). According to this model, the deep-sea environment is much more predictable than that of the continental shelf and supports a "biologically accommodated" fauna. Shelf faunas, on the other hand, are in more stressful environments and are therefore predominately "physically controlled" (Sanders, 1968). Given time, it is hypothesized, these stable environments will accumulate many stenotopic (narrow niched) species whereas shelf environments will be characterized by fewer, more eurytopic species. Original formulations of the hypothesis did not consider the generation of diversity, only its maintenance, but Slobodkin and Sanders (1969) attempted to argue that stenotopic species in the predictable environments would have a higher probability of speciating than would eurytopes in unpredictable situations.

The time-stability hypothesis has not been accepted by some ecologists, particularly because it is difficult to test (Peters, 1976; Abele & Walters, 1979a). Yet alternative explanations have also been ecological and equally difficult to test. Rex (1981a, 1981b) has adopted the "competitive equilibrium" model of Huston (1979) to explain the increased diversity of deep-sea communities. At equilibrium, competition is assumed to eliminate some species, thus lowering diversity. Communities in competitive nonequilibrium, in contrast, are said to maintain higher diversities (curiously, other ecologists have argued that communities in "competitive equilibrium" result in narrower niches and thus more species; e.g., MacArthur, 1965, 1969, 1972). Rex (1981a: 336–338) postulated that the higher diversity of predators on the slope and rise prevents competitive equilibrium, thus raising diversity (see also Rex, 1976).

As Rex (1981a: 338) noted, this hypothesis could account only for the maintenance of diversity, so the problem still remains why there are more species at increased depth, including more predators. Not only does the hypothesis fail to address the question of speciation and extinction rates in a predictive manner, but whether the hypothesis is amenable to empirical evaluation also needs to be considered. How, for example, might one determine whether these deep-sea communities are at equilibrium or not? And, how might the predicted historical roles of competition and predation be evaluated in communities located at depths of 1,500–3,000 meters?

The critical weakness with these ecological hypotheses is that they do not explain gradients in speciation and extinction rates that must exist from the continental shelf to the deep-sea. As discussed earlier, a simpler hypothesis exists: namely, that continental slopes are regions of high geomorphological complexity and that this has promoted a higher rate of speciation. Whether these deep-sea environments have had lower extinction rates than those of the continental shelf or abyssal plain is an open question. Predictability and stability do not imply that an environment will necessarily be more favorable in a physiological sense than are less stable environments, although we might expect greater stability to contribute to lowering the probability of extinction. The time-stability hypothesis, if it has validity or usefulness, would seem to speak only to the issue of a possible difference in extinction rates between environments of the shelf as compared to those of the slope. Present considerations suggest that the deep-sea diversity gradient is better explained by a nonecological

hypothesis that emphasizes variation in speciation and extinction rates.

Conclusions

Conventional interpretations of biological diversification generally are characterized by assumptions that the biosphere is at or near some global equilibrium, that gradients in diversity can be explained by ecological theories of community dynamics, and therefore that speciation and extinction are diversity-dependent. This paper presents an alternative conceptualization of biological diversification and its causes. Some of the main arguments underlying that conceptualization include:

1. The biosphere is a nonequilibrial thermodynamic system, open to a flux of energy and matter from outside the system. The energy-flow from the sun drives biosphere evolution through the transductive capabilities of organisms, namely reproduction and ontogeny. New matter enters the biosphere primarily as a result of the chemical breakdown of the outer surface of the lithosphere.

2. Because the biosphere is an open system, biomass would be expected to increase through time, subject to constraints originating from outside the system. Such constraints would include the physical and chemical properties of the earth and its history.

3. Patterns of diversity are a first-order function of rates of speciation and extinction.

4. The rates of speciation and extinction are diversity-independent. The rate of speciation is hypothesized to be mediated by the rate-change of lithospheric evolution operating through geomorphological complexity. Increased complexity presents more opportunities for vicariance and long-distance dispersal to produce isolation and differentiation.

A deterministic theory of extinction is formulated and relates an increased probability of extinction to an increase in the gradient of environmental harshness. The latter is a measure of the physiological stress to which populations are exposed.

5. The theory of diversification proposed here is testable and has considerable empirical support. Latitudinal and longitudinal gradients of diversity, in both terrestrial and marine environments, can be explained most simply by variation in lithospheric complexity and environmental harshness. The theory, as does any conjecture dealing with complex historical patterns, does not claim to explain all observations; rather, it attempts to account for the greatest amount of variance seen in large-scale diversity gradients.

6. Because the biosphere is an open thermodynamic system, we would not expect the Phanerozoic species diversity curve to show stability, except perhaps over short time periods, and then only because outside constraints (extinction) are damping diversification. Present data support the hypothesis that diversity has not yet reached an upper limit. The exponential rise of the curve itself can be "reset" by mass extinctions or it can be "calibrated" by constraints imposed from outside the system, e.g., by major shifts in global harshness, which might increase the gradient in background extinction.

7. Ecological theories proposed to explain large-scale gradients in diversity have been unsatisfactory because they do not address the first-order causes of these gradients, namely geographic variation in the rates of speciation and extinction. Assumed ecological correlates of high diversity (greater niche specialization and niche overlap, changes in the intensity of competition, increased predation), even if they do exist, are postulated here to be effects of that diversity, not its first-order cause.

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